ECOLOGY

Vol. 37 JANUARY, 1956 No. 1

ALTITUDINAL AND MICROCLIMATIC RELATIONSHIPS OF SOIL TEMPERATURE UNDER NATURAL VEGETATION[1]

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This study is concerned with an evaluation of soil temperature data taken at intervals of approximately one week from late January to November, 1950, in a series of forest stands in the Great Smoky Mountains of Tennessee and North Carolina in which tree growth studies were being made. The stations varied in altitude from 1500 to 6000 feet and were located near the Park Headquarters—Newfound Gap—Clingmans Dome Highway, along which the four weather stations of the Smoky Mountain Snowfall Study earlier discussed (Shanks 1954b) were also situated.

These data were at first collected for their intrinsic value as temperature samples in the root zone of the respective habitats, but it was soon discovered that their trends were similar to the air temperature trends as measured by the weather stations and by maximum-minimum thermometers exposed at the one-foot level facing north. It was also found that in the typically closed forest stands of this area, soil temperatures and air temperatures in contrasting adjacent habitats showed similar microclimatic differences.

Nature of Data

Soil temperatures reported in this paper, except where otherwise noted, were taken with a Weston dial-type metallic thermometer with 8-inch stem, of which the terminal 2 inches is supposed to be inserted in the solid or liquid medium to be checked. It was the practice to insert the thermometer in the soil through natural litter cover to a depth of 7 inches, so that the terminal 2 inches would center at 6-inch depth, and to leave the instrument in position until the dial reading became constant. This usually required about one minute. The smallest graduation on the dial was 2°F., and readings were commonly made to the nearest 0.5°F. Three such readings were taken within a few feet of the reference air temperature station, wherever the soil was of sufficient depth. Ranges of the sets of three readings are summarized in Table I. The median value of each set was used in subsequent computations. Further analysis of the data reveals that 14.2% of the sets had a range of zero, in 65.7% of the sets at least 2 of the 3 readings agreed, and only 5.9% of the 1017 individual readings differed from the median of the set by more than one degree F. If station No. 7, at the Newfound Gap weather station, which does not have forest cover, is excluded, these values are changed to 15.8%, 70.5%, and 4.6%, respectively. Station No. 6, which is in an isolated spruce-fir stand at 4000 feet, is on such a rocky site that it is difficult to find sample points with satisfactory soil depths, and the variability at this station is actually a reflection of local microclimatic variation within a radius of about 50 feet under varying forest cover.

Table I. Ranges among sets of three soil temperature readings, Great Smoky Mountains, February-October, 1951

Station no.	Feet alt.	Range in degrees F.							Mean range	Total no. of sets
		0	0.5	1.0	1.5	2.0	2.5	2.5+		
1......	1500	5	16	11	2	—	1	—	0.7	35
2......	3200	5	9	10	1	4	—	—	0.83	29
3......	3400	6	11	11	5	1	—	2	0.9	36
4......	3400	6	8	10	7	4	1	—	0.97	36
5......	3800	4	7	7	11	6	—	1	1.18	36
6......	4000	1	5	12	3	7	1	5	1.56	34
7......	5000	—	2	8	5	8	4	9	2.18	36
8......	5200	6	12	9	3	1	—	1	0.8	32
9......	5200	7	10	11	—	2	—	—	0.67	30
10......	6000	8	12	10	3	1	1	—	0.71	35
Total....	....	48	92	99	40	34	8	18	1.06	339
		Excluding station No. 7							.93	303

It appears that in the Great Smoky Mountains under closed forest cover, *when soil is present,* even single soil temperature readings may make up a sufficiently representative sample to indicate microclimatic variation with altitude, site, exposure, and type of cover.

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[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 161. The field work was supported in part by a Sigma Xi Grant.

Evaluation of Instruments

Since it was evident that soil temperatures taken with the metallic thermometer could be reliably used to differentiate habitats, the 1951 data were taken without detailed study of the characteristics of the instruments. This evaluative study was undertaken September-November, 1953, at the writer's residence, 319 Hermitage Road, Knoxville, under a second-growth oak-hickory stand at an altitude of 980 feet. It consisted of a comparison of readings from the metallic thermometer, mercury-in-glass laboratory thermometers, and thermocouples, installed in a natural forest soil under forest cover and normal forest litter.

Thermometers were selected for agreement with each other and with thermocouple readings in a water bath at room temperature. The metallic thermometer was of the dial type previously described, range 0 to 140°F.; the standard mercury-in-glass laboratory thermometer had a range −10 to 60°C.; copper-constantan thermocouples, #30 wire, were read with a Leeds and Northrup compensated reference junction potentiometer. The installation included an exposed Sixe's type maximum-minimum thermometer mounted horizontally facing north at one foot above the ground, a thermocouple adjacent to this thermometer bulb at one-foot level, a thermocouple at the surface of the A_1 horizon of the soil beneath about 1½ inches of forest-floor organic matter, and a series of thermocouples at depths of 1, 3, 5, 6 and 7 inches, adjacent to the stem of the metallic soil thermometer. The thermocouples were installed in holes made with an ice pick at the side of a small soil pit without otherwise disturbing the soil profile, and the glass thermometer was installed horizontally from this pit at 6-inch depth. The pit was then filled except for a shaft about 3 inches in diameter, which was covered with a cardboard lid supporting the original litter cover. The lid was removed only for thermometer readings.

The comparison summarized in Figure 1 is based on 30 sets of readings taken 29 September-13 October, 1953, in the temperature range between 59 and 68°F. There is no evidence that the metallic thermometer is less reliable than the glass thermometer. It also appears that the mean of a 5-, 6-, 7-inch thermocouple series may provide a slightly better estimate of temperature at 6-inch depth than a single 6-inch reading. This should follow from the fact that in almost every case (see Figure 3) the temperature profile through the 5-, 6-, 7-inch depth is smooth, with the median reading of the three falling at 6 inches, and the use of mean value would tend to smooth out reading errors.

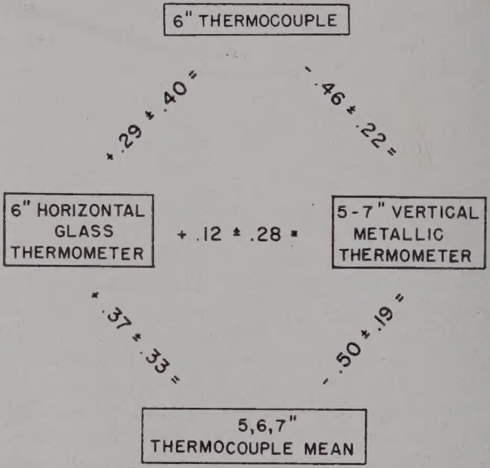

Fig. 1. Comparison of soil temperature readings by metallic thermometer, mercury-in-glass thermometer, and thermocouple, under forest cover near Knoxville, Tennessee, 29 September-13 October, 1953.

The relationship between readings of the metallic soil thermometer and the 5-, 6-, 7-inch thermocouple mean used as standard is illustrated in Figure 2, which is, in effect, a calibration of the metallic thermometer in terms of thermocouple readings. The central trend line is the calibration curve and the dashed lines represent the 95% confidence limits. It may be inferred that, once calibrated, such a metallic thermometer may be expected to yield values accurate within a half degree F. at the 95% confidence level.

Temperature Profiles as Related to Time of Reading

The transfer of heat past the soil-atmosphere interface under natural conditions is an extremely complex geophysical phenomenon. Conditions influencing it have been discussed in considerable detail by Geiger (1950) and workers cited in his extensive bibliography and in such general works as those of Keen (1931) and Baver (1948), and in briefer summary by Fitton and Brooks (1931), Daubenmire (1947), and Richards (1952). Both radiation and conduction are involved, as well as transfer by movement of warmer or colder air or water into or out of the soil.

Although cases are cited by Keen and Russell (1921) and Dreibelbis (1951), it is unlikely that the temperature at 6-inch depth is often greatly influenced by infiltration of warm or cold water.

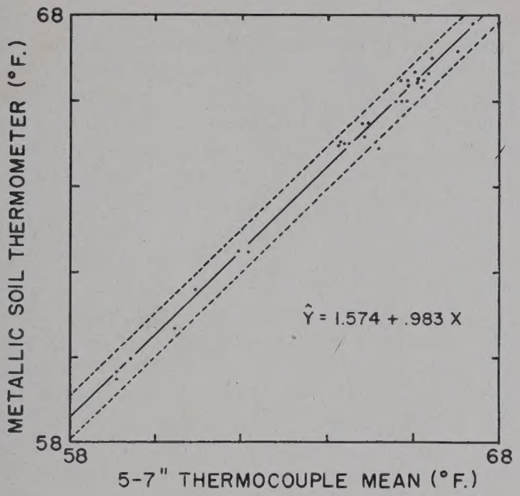

FIG. 2. Thermocouple calibration of metallic soil thermometer installed in forest soil, using data summarized in Figure 1.

Only with dry soil and heavy rains would a detectable change at 6-inch depth be produced, and even so the rain which warmed or cooled the soil would likewise warm or cool the air near the soil surface.

In the present case, under forest, relatively little direct radiation reaches the ground. Of the 82-95% of incident radiant energy which is absorbed by forest areas (Geiger 1950), a good deal is absorbed by the vegetation rather than by the soil. Most of the heat lost from a forest stand by radiation at night is also lost from the tree crowns. Geiger goes so far as to say, "Nocturnal cooling in an old stand is entirely a function of the outer active surface." The relatively slight radiation loss from the soil surface is principally to the lower surface of the canopy above, which transmits heat ineffectively, thus serving as an insulating layer.

The diurnal gain and nocturnal loss of heat by forest stands are not only thus damped by shrub and tree canopies, but are also quite effectively retarded by the litter and humus of the forest floor. As illustrated by Geiger (1950: 143, after W. Schmidt), leaf litter has an even lower heat conductivity than snow. The fact that it is an extremely effective insulating layer is responsible for the slight frost penetration under continuous litter characteristic of the greater part of the deciduous forest. Humus also contrasts with mineral soil in higher minimum temperature at corresponding depth, and longer frost persistence in the spring.

For these reasons, soil temperature profiles under natural forest canopy, and normal forest litter and humus layer, are quite different from the strong radiation-type profiles usually illustrated in the books (*e.g.,* Daubenmire 1947: 172, 174; Geiger 1950: 34). A series of profiles representing a period of cooling under the previously mentioned Hermitage Road oak-hickory stand is presented in Figure 3. The canopy trees were still in full leaf and the soil was quite dry at the time. The lag of maximum and minimum temperature with depth and decrease of range with depth are illustrated. Minimum air temperature had been reached by 0645, but minimum soil temperature at 6-inch depth would not be reached for another 4 or 5 hours, typically occurring about noon on a clear day. Maximum soil temperature was typically reached between 2100 and 2400 during the October-November period of observation. This is a similar lag to that reported in comparable studies by Fowells (1948), who reported a lag of about 5 hours in the minimum and about 7½ hours in the maximum at 7-inch depth in a pine forest in California, and Christy (1952) who, in discussing winter soil temperatures in a beech forest in central Ohio, reported that highest daily

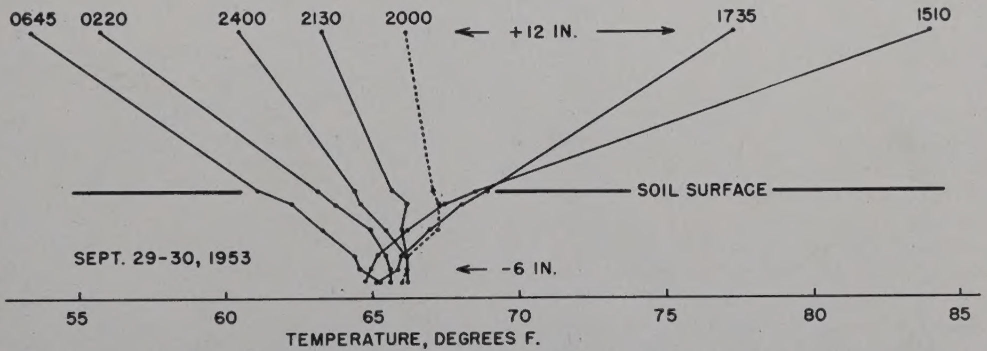

FIG. 3. Sample temperature profiles from the area from which the data of Figures 1 and 2 were taken.

temperatures at 6-inch depth occurred around midnight and lowest daily temperatures around noon.

Average daily temperature range at 6-inch depth at the Hermitage Road station was 1.5° F., maximum range 2.1°F., in a 16-day October-November sample. These data are consistent with those of other studies under forest cover. Fowells (1948) reported an average October range of 1.5°F. at 7-inch depth under Cailfornia pine forest, an average range of 2.3°F. for July. Li (1926) reported a range of 1.58°F. for October and 2.47°F. for July at 6-inch depth under old pine forest in New England. Christy (1952) reported that "daily temperature fluctations rarely are as much as three degrees" at 6-inch depth under an Ohio beech forest in summer. From these data and the fact that the mountain climates are generally more moist than the valley climates (Shanks 1954b), which would tend to result in less fluctuation in soil temperature (Fitton and Brooks 1931), it is inferred that time of day would introduce less than 1°F. error into the mountain soil temperature readings, and no attempt has been made to correct these readings for time of day. These readings were almost always taken in altitudinal series, which required an average of 5.25 hours for the 10 stations, so there is very little "time of reading" error between successive stations. It does appear, however, that the temperatures reported for any station would tend to average slightly lower than its true mean, for the readings were taken in daylight hours and most of them were taken nearer to the time of minimum than to the time of maximum.

Results, Great Smoky Mountains

Records from three of the official stations of the 1946-50 Smoky Mountains Snowfall Study have been selected for comparison with nearby soil temperature trends (Figure 4). Locations and topographic situations of these stations have been earlier described (Shanks 1954b). The 1500-foot soil temperature station was in the valley flat about a quarter-mile from the 1460-foot station at Park Headquarters, under a remnant stand of natural vegetation which included both hardwoods and pine; the 3800-foot soil temperature station corresponded with the air temperature station, and was shaded by rhododendron; the 6000-foot station was under a heavy natural stand of spruce and fir on a slope of less than 10° toward the south near the Clingmans Dome Highway about one-half mile from the Forney Ridge location of the 6300-foot weather station. Mean monthly soil temperatures based on readings at intervals of approximately one week were used. Values for January and November were not complete and were omitted as not representative.

The graphic comparison in Figure 4 illustrates the lag in spring warming of the soil which is very pronounced in the March-May period, the summer May-August period during which the soil and air temperature trends are relatively parallel at all three altitudes, and the lag in fall cooling of the soil from August on. It would appear that soil temperatures could be most reliably related to air temperatures during the May-August period.

It also appears that, in general, soil-air temperature differences tend to be greater in the high temperature range than at lower temperatures.

These observations suggested the comparison of

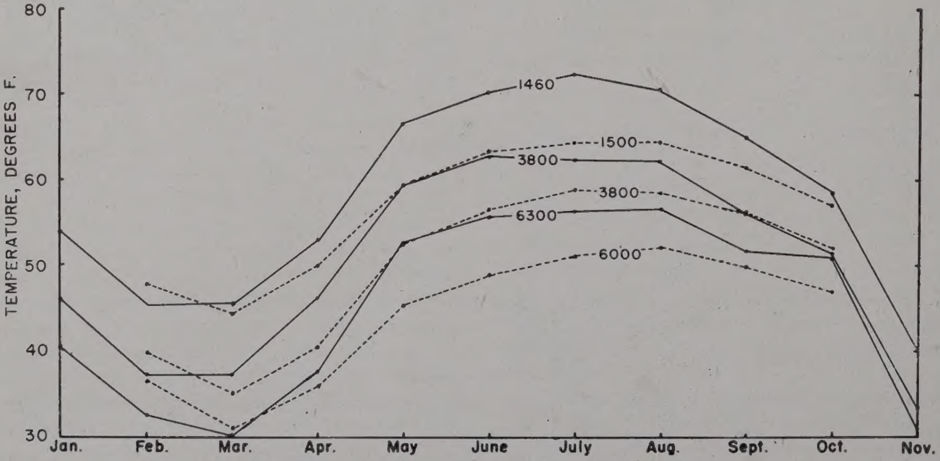

Fig. 4. Soil and air temperature trends at three altitudes, Great Smoky Mountains, 1950.

soil temperatures with standard weekly air temperature means embodied in Figure 5. Only values from May through August were used. The scatter of values from the fitted regression line provides an estimate of the reliability with which soil temperature may be used as a measure of air temperature. The *standard error of estimate* is ± 2.02°F. While this agreement is not precise, it is of interest to note that it is much closer than that expressed in the ± 3.05°F. obtained when the averages of weekly maximum and minimum temperatures from exposed thermometers are similarly compared with the same standard mean temperatures. However, it should be noted before abandoning the use of exposed thermometers that the maximum and minimum temperatures are themselves also useful information. It should also be stressed that the use of standard shelter data as a comparative standard is not meant to imply that standard shelter data are a more precise measure of plant environment than soil temperatures or temperatures taken with exposed thermometers at seedling level.

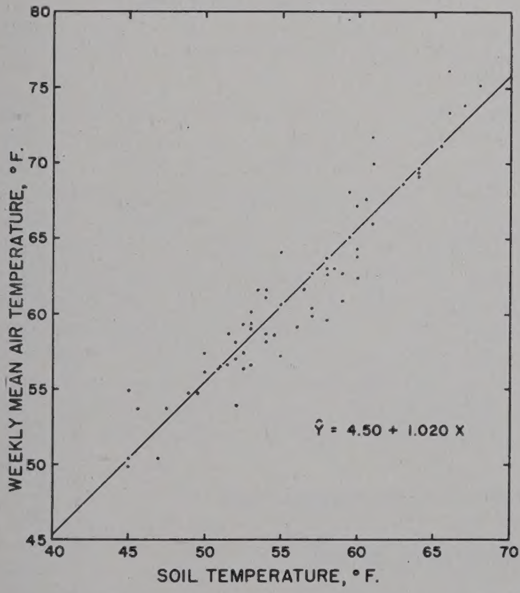

FIG. 5. Relationship between soil temperatures and mean weekly air temperatures, May-August, 1950.

While soil temperature appears to be reasonably useful as an approximate measure of air temperature under certain conditions, the usefulness of soil temperature does not rest on its precision as a measure of air temperature. Rather it depends on its capacity to measure environmental differences between contrasting topographic or altitudinal habitats. It is most promising as a relative measure, which can then be related to a standard weather installation at some point. The general agreement of altitudinal temperature lapse of soil and air is illustrated in Figure 6. This agreement is particularly good during the fall season. Even at the end of the unusually hot summer of 1954, a check profile, though considerably warmer at all points, closely paralleled the fall profiles of 1950 and that of mean air temperature.

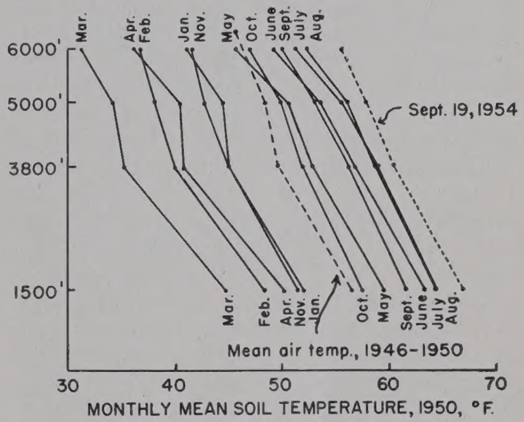

FIG. 6. Altitudinal profiles of soil temperature, Great Smoky Mountains, 1950.

Altitudinal soil and air temperature profiles for 1950 are further compared in Table II, in which the average slope of the curve is expressed in temperature decrease in degrees F. per thousand feet increase in altitude. Datum points are 1460 and 6300 feet for air temperatures, which are means of daily standard shelter data, and 1500 and 6000 feet for soil temperatures, which were taken about once a week. Agreement wavers due to several factors, but the April-September mean soil temperature difference is 2.95°F. per thousand feet, in essential agreement with the air temperature figure of 2.99°F. The highest soil temperature differences observed were 3.44°F. per thousand feet, in late April and early May, and the lowest value observed in spring or summer was a single value of 2.33°F. in mid-July.

The measurement of temperature differences in adjacent habitats differing in topographic position and in vegetation is illustrated in Figure 7. In each case, the reference line represents the soil temperature on the less variable site, on more convex topography, with largely evergreen vegetation, while the dots represent the departures of the adjacent coves, with their deciduous vegetation, from these reference values. In both cases, the general direction of slope is toward the south. In neither case is the up-slope tributary area of air

TABLE II. Decrease in soil and air temperature per thousand feet altitude, Great Smoky Mountains, 1950

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Air temperature, °F., standard data...	2.69	2.64	3.22	3.16	2.91	2.98	3.31	2.81	2.75	1.55	1.92	1.82
Soil temperature, °F., 6-inch depth...	2.33	2.51	2.98	3.11	3.11	3.18	2.95	2.76	2.60	2.33	2.22	–

drainage more than a few acres, nor is there any obstacle to free air drainage below. The stations of a pair are less than 60 yards apart and differ by less than 20 feet in altitude. The high-altitude example involves the contrast between a "beech gap" (Russell 1953; his Table IV is from the same gap) and the adjacent spruce-fir forest (Cain 1935, Oosting and Billings 1951, Shanks 1954a). The mid-altitude example illustrates the contrast between a buckeye-basswood-sugar maple cove forest (Shanks 1954a) and the adjacent hemlock forest with an understory of rhododendron, just above the lower tunnel on the Park Headquarters—Newfound Gap Highway. While relative effects of topography and contrasting vegetation cannot be isolated in either case, the microclimatic contrast in the seedling environment is clearly shown. The contrast is especially great in the spring before the canopy has closed, during the period of the great display of spring wild flowers. At this season the microclimatic contrast is the equivalent of more than a thousand feet of altitudinal difference, consistent with the fact that the spring flower displays of the beech gaps find their closest counterpart in the deciduous forest stands more than a thousand feet lower.

Selected mean monthly differences in microclimatic relationships among the ten stations established for tree growth studies in the Great Smoky Mountains are shown in Figure 8. The reference lines represent the average temperature lapse 1500-6000 feet, microclimatically warm habitats falling to their right and cool habitats to their left. The stations at 1500, 3800, and 6000 feet are those used in Figure 4 and the pairs identified by the letters A and B are those used in Figure 7. The 5000-foot station was at the location of the Newfound Gap weather station of the Smoky Mountain Snowfall Study. The 4000-foot station with its late spring refrigeration was in the low-altitude spruce-fir "island" described by Cooley (1954). The 3200-foot station was in the south-facing Fort Harry Cove, characterized by buckeye-basswood-sugar maple forest and noted for exceptionally early spring blooming of *Hepatica, Claytonia,* and *Phlox stolonifera.* It may be noted that on occasion the temperature of a cool station may correspond with the general temperature level 2000 feet higher (4000-foot station, March), or a

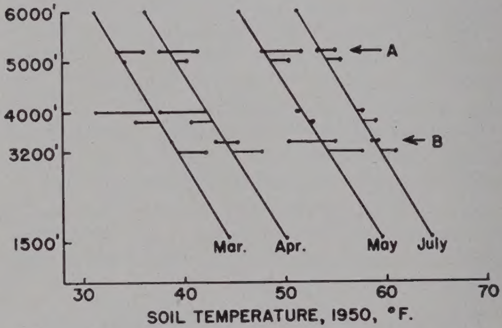

FIG. 8. Altitudinal profiles of selected mean monthly soil temperatures showing microclimatic departures of individual stations.

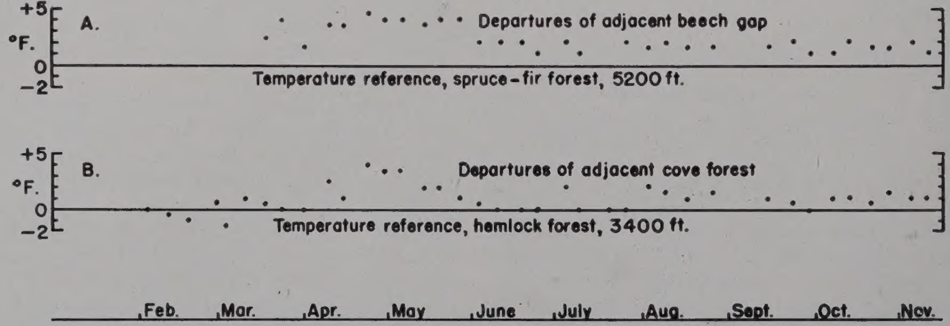

FIG. 7. Microclimatic variation in soil temperature in adjacent habitats differing in topographic position and forest type.

warm station may correspond with the general temperature level 1200 feet lower (5200-foot beech gap, May; *cf.* Figure 7).

Conclusion

Under the weather conditions prevalent in the Great Smoky Mountains and presumably in the Southern Appalachian region in general, and within the closed forest types generally characteristic of the region, soil temperatures taken with a dial-type metallic thermometer at 6-inch depth appear to provide a convenient and useful index of environmental differences. They are sensitive enough to measure differences between contrasting adjacent habitats. They are consistent enough that considerable confidence may be placed in a single series of comparative measurements. During the growing season and early fall the altitudinal profile of soil temperature parallels that of mean air temperature, and when related to mean air temperature at one altitude may be used to estimate mean air temperature at another altitude with reasonable precision. The soil thermometer thus promises to be a useful instrument for the study of topographic pattern of microclimatic variation and its relationship to altitudinal climatic gradient, essential elements in the bioclimatology of mountain or hill country.

Summary

Soil temperature data from 6-inch depth at weekly intervals provide a useful index to altitudinal and microclimatic temperature differences in the closed forest vegetation of the Great Smoky Mountains, correlating more closely than the means of weekly maximum and minimum air temperatures with standard weather record means. The lag in heat transfer is such that the soil temperatures constitute a useful integration of radiation and air temperature conditions during the preceding week.

Instruments and measurement procedures were evaluated. Thermocouple calibration gave no evidence that the metallic thermometer was less reliable than standard mercury-in-glass thermometers. Variation from the median within sets of three readings exceeded 1°F. in only 5.9% of the cases. Time of day appeared to introduce less than 1°F. error into the series of readings.

This degree of precision was adequate to reveal microclimatic differences between adjacent habitats which differed in vegetation, such as the beech gaps and adjacent spruce forests, or deciduous coves and adjacent hemlock forests. Microclimatic temperature differences were recorded which on occasion were the equivalent of as much as 2000 feet of altitudinal temperature difference.

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COMPETITION AND SUCCESSION ON A ROCKY MOUNTAIN FELLFIELD

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Introduction

During work in Alaska, in the northern Rocky Mountains, and in the mountains of northeastern America which led to conclusions and publications on timberlines (Griggs 1934a, 1938, 1946) the ecology of the tundra beyond the tree limit was always in the background of my study and thinking. Throughout this work I devoted more time and effort to studying the arctic-alpine vegetation beyond the trees than to timberline itself. But I was unable to resolve to my own satisfaction the problem of the tundra. (Griggs 1934b, 1936.)

I am not the only one who has been baffled in his effort to understand arctic-alpine vegetation. Weaver and Clements (1938) say, "The tundra climax consists chiefly of four communities, the successional relations of which are little understood as yet." That is to say: The many seasons that Clements spent at his Alpine Laboratory in Colorado did not bring to him a satisfactory understanding of the tundra.

In his great work on the Botany of the Canadian Eastern Arctic (Polunin 1948: 3) remarks, concerning the analagous situation in the Arctic Archipelago: "The more I learned about the vegetation as a whole, the less I felt inclined to generalize about it for if one impression stands out from among all my studies of the vegetation of the Canadian Eastern Arctic, it is that of extreme (and often to me inexplicable) variability from place to place. Certainly there will long remain a great deal more to discover: nor is our knowledge as yet nearly sufficient to allow of detailed comparison with other arctic or subarctic lands." Whitehead (1951: 349) begins his discussion with the observation, "Relatively little ecological work appears to have been done on mountain summit regions, other than descriptions of vegetation."

It is clear enough that the methods of conventional ecology as it has developed in the temperate zone have not led to a satisfactory solution of the problem of arctic-alpine vegetation. I am therefore trying a new approach which can, I believe, lead us into a sound understanding of arctic-alpine ecology.

Much of the trouble arises, so it seems to me, from premature attempts to deal with arctic-alpine regions from the point of view of synecology. Autecology offers a simpler, less complicated approach. Study has convinced me that only when we understand the ecology of individual arctic or alpine species can we synthesize an understanding of arctic-alpine vegetation. I am therefore studying the tundra, species by species.

The approach used resembles somewhat that adopted by Oosting and his associates (Keever, Oosting, and Anderson 1951) in studying succession on exposed granite rocks.

My studies were made during the open seasons of 1952, 1953, 1954, and 1955.

For the present, however, I am concentrating my attention on fellfields and habitats transitional from fellfields where the plants stand apart from each other. The reason for this decision will be evident to anyone who examines a small area, say a square foot, of closed or partly closed tundra. He observes several to many species growing together. Doubtless an intense struggle for survival is going on among those plants but it is extremely difficult to find means of assessing the relative potencies in the struggle of the species present.

But on the bare gravel of the fellfield each individual plant has its own struggle for existence uncomplicated with others. That is, it is uncomplicated unless other plants happen to invade the area. Then the struggle is a relatively simple duel whose progress may be watched with comparative ease over the years even though we have as yet little inkling as to the character of the "weapons" each species brings to the contest.

The present study is an attempt to elucidate the stages in this struggle on a particular fellfield. It is hoped that this study may invite comparisons with other fellfields and so set the stage for comparative ecology of arctic-alpine regions. Also it is hoped that study of the fellfield may lead to an understanding of the higher stages in the succession.

Location of Study

The alpine tundra of the Rocky Mountain National Park presents an exceptionally favorable opportunity for such study. Here, between timberline which lies at about 11,500 feet (3500 m.) and the high points culminating in Long's Peak, 14,255 feet (4350 m.), is a comparatively flat peneplain. The gentle slopes of this old erosion surface, in contrast to the steep unstable surfaces of most mountains, have permitted the development of a deep soil in places. This is clothed with a tundra which is near the climax for the region. In places of steeper slope or greater exposure to high winds, this shades off into fellfield and rock slide. There are many square miles of this rolling plateau above timberline.

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[1] Collaborator, U. S. National Park Service.

Study of this high country is very greatly facilitated by the Trail Ridge Road, a modern highway, U. S. 34, which traverses it. Eleven miles (18 km.) of this highway are above timberline, 4 miles (6 km.) of it are above 12,000 feet (3700 m.). It is the highest through highway in America.

The road is opened by high power rotary snow plows in the spring about May 30, before there is any sign of growth in the plants and the endeavor is to keep it open in the autumn until after the growing season has ended.

This effort is however only partly successful. It is not unusual for the road to be closed for short periods by snow or ice through June or even late in July.

It is an essential prerequisite to any ecological interpretation of vegetation that the natural condition of the area selected for study be known; and for a subject as little understood as arctic-alpine ecology, it is almost essential that the vegetation studied be in an untouched, primitive condition.

Many of the high places above timberline both in this country and abroad have been so heavily grazed that their present condition differs widely from the primitive. The botanist examining Tuolumne Meadows in the Yosemite, for example, is greatly disappointed at the relative poverty of the flora. The explanation lies, it is believed, in the fact that for many years Tuolumne Meadows were heavily grazed by sheep.

I am informed by Richard M. Leonard, President of the Sierra Club, that in 1895 there were 295,000 sheep within the limits of Yosemite Park. Although they were driven out in that year, the vegetation, in 60 years, has not regained its primitive condition.

To my eyes, the tundra on Trail Ridge seems as undisturbed as the vegetation which I have studied on uninhabited areas of the Alaska Peninsula.

ACKNOWLEDGMENTS

In addition to these advantages of the area, natural and man-made, I was fortunate in having a third of equal importance—very cordial cooperation and assistance from the staff of the Rocky Mountain National Park. I, and the work, owe a great debt to Supt. David Canfield and his successor, James V. Lloyd, to Asst. Supt. Francis D. La Noue, Chief Ranger Barton Herschler, Park Naturalist E. C. Alberts, Ranger Loren Lane and others without whose assistance the work could hardly have been carried through.

A further prerequisite to my undertaking was the taxonomic background. When the work began in 1952 all the publications dealing with the flora of Colorado were out of print. But the botanists of the region were hard at work to remedy the deficiency. In the interval, three floristic works, each excellent in its own field, have appeared. From the University of Wyoming, Mrs. Nelson's revised "Plants of the Rocky Mountain National Park," profusely illustrated; from the University of Colorado, Wm. A. Weber's "Plants of the Colorado Front Range"; from the Colorado State College, H. D. Harrington's "Manual of the Plants of Colorado." Each of the Colorado authors has been most helpful to me and I appreciate it greatly.

NOMENCLATURE

The pioneer Rocky Mountain botanists were surprised and astonished at the similarity of the high tundra flora to that of the arctic and of the Alps. Under the lead of Joseph Dalton Hooker whose great paper on the distribution of the arctic flora laid the foundation for the science of plant geography, they emphasized the cosmopolitan character of the high mountain flora of Colorado.

These men were followed by a generation of "splitters" who saw in very many of our alpine plants new endemic species peculiar to the Rocky Mountains. The horde of new species names they coined, however well they might be justified on strictly taxonomic grounds, thus concealed the fundamental geographic relationships of our flora.

The present generation of Colorado botanists have reduced to synonomy a large proportion of the "new species" thus claimed as endemics. Many more have been questioned and set aside for careful revision. Thus, *Anemone narcissiflora* L. was considered a wide ranging species extending from the Alps across Siberia, through Alaska and south into our montains. But A. Nelson described its Rocky Mountain representative as *A. zephyra.* Of this Harrington says: "Critical study may indicate that our plant should be *A. narcissiflora* L." Weber lists it under this original Linnean name. This is the only way to bring out the geographical and perhaps the ecological relations of these anemones. A similar case is *Festuca brachyphylla* as it is called by botanists dealing with the northeastern portion of North America. This "species" is not mentioned by Weber but Harrington reveals the facts of the case when he lists this, probably the most abundant grass of the tundra as a variety of the familiar cosmopolitan sheep fescue, namely *Festuca ovina* var. *brachyphylla* (Schult.) Piper.

The ecologist needs, I believe so to choose his nomenclature that, as far as practicable it will reveal without circumlocution the relationships of the plants he deals with.

OBSERVATIONS

I. *Silene acaulis*

(Fig. 1)

If asked to name the one most characteristic arctic-alpine plant more people would perhaps choose *Silene acaulis* L. than any other species.

In our region it is a dense round pancake of a plant spreading radially flat on the ground or bulging up into a flat dome from a cluster of strong tap roots. At flowering time, the whole surface of its cushion is sprinkled, sometimes completely covered with scores of pink or whitish sessile blossoms half an inch in diameter.

It occurs in almost every arctic and alpine habitat. It is native not only on the Rocky Mountains as far south as New Mexico and Arizona but throughout much of Alaska into eastern Siberia, across the Barren Grounds of Canada, south to Mt. Washington, New Hampshire, almost everywhere in the Arctic Islands, over Greenland, Spitzbergen, Lapland, the Alps, the high Apennines as far south as Rome, and the Pyrenees. In Greenland, it goes clear to the north coast in latitude 83°6′ which is within 25 miles of the northernmost locality reached by flowering plants anywhere on earth (Polunin 1940).

Throughout its vast range it is a single taxonomic entity with little variation except in the length of the peduncle, calyx, and capsule. Throughout America, the flowers are sessile or subsessile and the calyx and capsule short, variety *excapa*. In other regions, the peduncles may become 4 cm. long. But is this wide ranging species sufficiently homogeneous ecologically to permit of intelligent discussion as though it were always ecologically equivalent? Perhaps a part of the confusion of arctic-alpine ecology arises from a habit of assuming that taxonomic uniformity implies ecologic uniformity. But this implicit inference does not rest on much explicit evidence. It should be examined critically.

In the tundra of the Rocky Mountain National Park, *Silene acaulis* is the most aggressive of pioneer plants. On high altitude ground laid bare by road building, *Silene acaulis* is the most frequent colonist. Sometimes 80 or 90 per cent of the new plant population is of this species. Plants of all ages down to minute seedlings are abundant—more abundant in denuded habitats than on the undisturbed tundra.

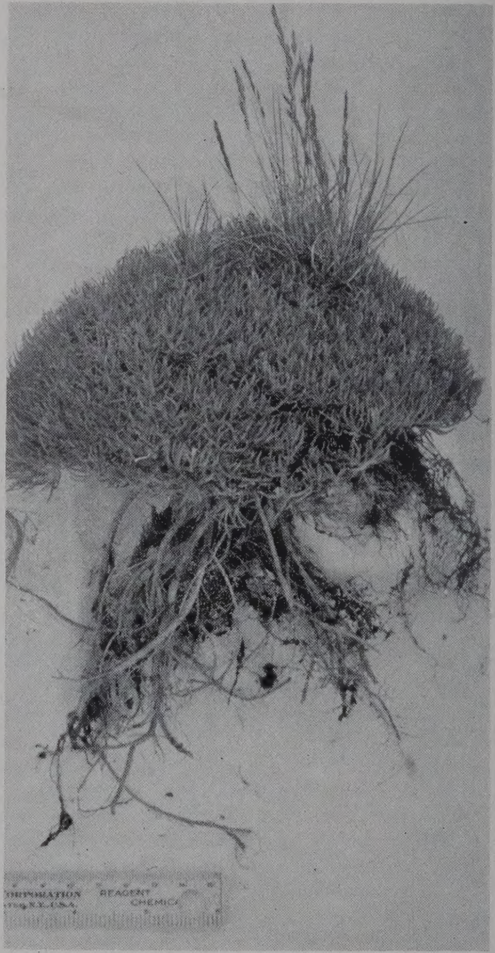

FIG. 1. A tussock of *Silene acaulis* invaded by *Festuca ovina brachyphylla*. As it grew appressed to the ground the tussock was a flat disc about 10 inches across. The fine black fibrous roots of the invader at the right had established themselves in soil free from roots of the host. The numerous host roots, broken off at about 8 inches, originate at the crown about an inch below the surface.

Although a slow grower as compared with the weeds we are accustomed to see in open land at low altitudes, *Silene acaulis* grows fairly rapidly for a fellfield plant. On ground denuded by road building 23 years ago, cushions of *Silene* 10 inches (25 cm.) in diameter are not uncommon; one 14 inches (35 cm.) was measured; another 15 inches (37.5 cm.). A third, 17 inches (42.5 cm.) in diameter was observed. But this was at the edge of the disturbed ground and was probably older than the disturbance. It was moreover in process of dying out. These dimensions are fully up to the maximum observed in adjacent undisturbed tundra where, in competition with other established plants, the average size of *Silene* cushions is nearer 6 inches (15 cm.) than 12 inches (30 cm.).

As is well-known, *Silene acaulis* is supported by a very long and strong but much branched tap root or a cluster of tap roots. Schroeter (1926: 789) reports that these roots may reach lengths of 70-130 cm. according to the observations of Wetter. This far exceeds Daubenmire's figures (1941). The diagrams accompanying Schroeter's statement suggest however that Wetter's measurements may have been taken from crevice plants rather than from specimens growing in the soil—as they do on Trail Ridge.

As will appear however, *Silene acaulis* has by no means the strongest root system of the fellfield plants. Its roots would in fact seem to put it under a disadvantage against some of its competitors; compare Figures 1, 3, 5.

All the characteristic species of the fellfield colonize bare ground; they are pioneers. Thus, an ecologist intent on understanding the climax, after recognizing them as pioneers is apt to pass on to the study of plants higher in the succession without giving them further consideration.

But there are marked differences in the ecological status of the fellfield pioneers and there are clear criteria for differentiating among them.

Almost all the forbs of the tundra arise from seed. Only a few spread extensively by vegetative offshoots as was pointed out by Daubenmire (1941). In the open tundra away from rock crevices, there are neither berries nor burrs. The seeds of almost every species of the fellfield fly before the high winds characteristic of the area and probably are caught in every situation that provides lodgment. Many of them are caught in the foliage of old cushion plants. One might well suppose, *á priori,* that a germinating seedling would have little chance of gaining a foothold in a dense mat of thrifty deep-rooted vegetation. But this is not the case. A large proportion of the new plants that succeed in establishing themselves come up within the cushions of old plants which they push out of the way as they grow.

Silene acaulis is a leading host to such intruders, 33 species of which, as follows, were found invading it. And the list is by no means complete.

Arenaria obtusiloba (Rydb.) Fernald
Draba crassifolia R. Grah.
Thlaspi alpestre L.
(In this case perhaps *Silene* was dominant. The stems of the two were closely intertwined. Both are pioneers on bare ground.)
Arenaria rubella (Wahl.) Sm.
Anemone narcissiflora L.
Salix nivalis Hook.
Phlox caespitosa Nutt. (by runners)
Cerastium sp. (cf. *beeringianum* C. and S.)
Draba fladnizensis Wulf.
Paronychia pulvinata Gray
Saxifraga chrysantha Engelm.
S. rhomboidea Greene
Chionophila jamesii Benth.
Androsace septentrionalis subumbellata A. Nels.
Mertensia viridis A. Nels.?
(one small seedling not yet surely identifiable but surely invading.)
Trifolium nanum Torr.
Polygonum bistortoides Pursh
P. viviparum L.
Draba aurea Vahl
Primula angustifolia Torr.
Eritrichium elongatum (Rydb.) Wight
Festuca ovina brachyphylla (Schult.) Piper (Fig. 1)
Sedum stenopetalum Pursh (by runners)
Poa spp.
Luzula spicata (L.) DC.
Haplopappus pygmaeus (T. and G.) Gray
Erigeron spp.
Carex scopulorum Holm
Carex spp.
Artemisia scopulorum Gray
Castilleja occidentalis Torr.
Hymenoxys grandiflora (Pursh) Parker
Geum rossii (R. Br.) Ser.

The seed from which these invaders arise must be broadcast indiscriminately but there is nothing indiscriminate about their survival. Seeds of *Silene* must lodge in the bodies of the species which invade it as surely as their seeds come to *Silene*. But *Silene* does not grow there. Among the hundreds of invaders observed, only a very few cases were seen where the roles of invader and host were reversed. The species listed were repeatedly seen invading *Silene* but *Silene* was seen invading others only three or four times.

In other regions it has been reported that cushions of *Silene acaulis* harbor foreign species. On flood plains of Norwegian Lapland, Polunin (1936: 384) describes *Silene acaulis* as growing until the tussocks "may be as much as a meter in diameter and one-half meter high" so that willow seedlings can start in their shelter.

In the Apennines at altitudes around 9,000 ft. (2500-2800 m.) Whitehead (1951) speaks of *Silene acaulis* as "often with secondary colonization." He lists 17 species which commonly occur either as colonists of *Silene* cushions or as growing in their shelter. In some cases, as with *Festuca dura, Silene* disappears leaving only the ring or semicircle of *Festuca* (his Fig. 5). Whitehead draws no particular distinction between the plants which colonize *Silene* and those which merely grow in the shelter afforded by its cushions, as they might behind a rock. But to me there seems likely to be an important difference. *A priori,* one reasons that plants growing near *Silene* may be free from direct competition by roots or otherwise, with the plant that shelters them but colonists which ultimately displace their hosts must compete with them. My observations have not yet been carried on long enough to prove the point but photographs of the same plant in successive years suggest that plants adpacent to *Silene* cushions grow more rapidly than invaders within their borders.

In his latest paper on Arctic botany (1955), Polunin reveals increased awareness of the problems discussed in this paper when he says, "Some plants appear to become established only in the shelter afforded by others for example actually in the tussocks of the moss campion (*Silene acaulis*)" and again, "Unfortunately the study of the ecology of individual forms has not been stressed in the Arctic." But he neither names any specific invaders of *Silene* nor suggests that other hosts are also invaded.

Quite aside from its obvious competitive relations with invaders, there is some evidence which suggests that *Silene acaulis* in different regions is far from uniform in its ecological behavior. On Mt. Washington in New Hampshire, for example, it is by no means the aggressive colonizer that it is in Rocky Mountain National Park. There it has been known for a century from a single small station but manifests no tendency to spread into other habitats either on disturbed or undisturbed ground. The cushions are comparatively small. According to C. J. Lyon and Frederic P. Lord (personal communication) 8 inches (2 dm.) across is a maximum on Mt. Washington.

In Alaska, *Silene acaulis* grows at sea level on both north and south coasts. The tussocks are generally small—about the size attained on Mt. Washington. But under some circumstances, they grow much larger. Dr. George H. Ward writes me that he took Kodachromes of *Silene acaulis* "approximately 2 feet across and about 10 inches high as shown by a 6 inch ruler which I included in the pictures. I would say that this is close to a maximum size of the cushion for this locality—a sand dune area along the Meade River ca. 50 miles south of Point Barrow, Alaska, North 70° 40′, 156° 55′ West. These cushions roughly hemispherical in shape were formed wherever the plants were growing in loose sand. In sand that was fully stabilized it was only one of a large number of species forming a dense mat of vegetation; individual *Silene* plants were not nearly so large here. . . . Along the Utukok River at 1500 ft. elevation (North 68° 58′, 161° 12′ West) I found *Silene acaulis* growing in the gravel of small segmented polygons on the top of a ridge. These plants though did not form raised cushions and were not over 6 inches across."

In as much as he plans to continue this line of research the author would appreciate similar letters describing the habits of *Silene acaulis* in other parts of the world.

Whitehead (1951, Fig. 6) as well as Polunin describes *Silene* cushions a meter in diameter—nearly flat.

But Schroeter (1926) figures a cushion 50 cm. across and 18 cm. high from the Gornergratz in Switzerland and another almost spherical about 50 cm. in diameter from the Tatra Mountains of Poland. This is estimated as a century old.

These diverse plant bodies produce radically different conditions of life for the plants concerned, both hosts and invaders, in ways that were summarized long ago by Schroeter (1926).

The question is: are the different plant bodies due to differing conditions in the environment or do they come from genetic diversities within the group that we call *Silene acaulis?* It is appropriate then to emphasize the danger that in attempting to generalize about arctic-alpine ecology we may very likely be dealing with a situation where both environmental and genetic factors are involved as Clausen, Keck, and Hiesey (1948 and other papers) have found in their classic transplant studies, *e.g.,* with the various types of the polymorphic species of *Achillea.*

Diversity of arctic-alpine climates.—It should be noted that the climates of the vast area of country inhabited by *Silene acaulis* and by many other arctic-alpine plants as well are very diverse.

For high mountains, the Front Range of the Rockies on which the Park is located enjoys an unusual amount of "good" weather. Its climate is strongly continental, characterized by great and suddenly changing extremes with high winds. No systematic record of weather conditions is available for Trail Ridge but Cox's (1933) observations through two growing seasons on James Peak about 25 miles south of Trail Ridge give a sufficiently accurate idea of the summer climate of our area.

No generalizations however can be drawn from a short period of observation. Each of the four seasons in which I have studied on Trail Ridge has differed markedly from the other three.

Presumably, moreover, available climatic data will be greatly improved by the publication of the two sets of records being secured (1) by the University of Colorado's Institute of Arctic and Alpine Ecology, John W. Marr, Director, working in the vicinity of Arapahoe Peak about 20 miles south of Rocky Mountain Park, and (2) by W. D. Billings and L. C. Bliss of Duke University working in the Medicine Bow Range about 75 miles north of Trail Ridge.

Perhaps the most significant thing to be noted about the climate is that frost may be expected at frequent intervals throughout the year. There is no regularity in the frost-free season. Minimum winter temperatures are very low, lower than at many arctic stations. The highest temperature on bright summer days is about 70°F but such genial warmth occurs only briefly. Often before noon clouds appear and a local thunderstorm accompanied by a marked drop in temperature and high wind comes on.

Winds of gale force, 35-50 m.p.h., are of almost daily occurrence. But during my stays I experienced no winds approaching hurricane violence, 75 m.p.h. or more, such as are common on Mt. Washington in New Hampshire. The wind and the altitude greatly increase evaporation and, with it, water-loss from the plants.

It is well known that at the surface of the ground the zone in which *Silene acaulis* grows, air movement is much less and temperature, when the sun shines, much higher than above the ground. These circumstances undoubtedly largely account for the fact that none but prostrate and cushion plants can grow on the fellfield. Few plants anywhere on the high tundra except in the shelter of a rock grow as much as a foot tall.

In southwestern Alaska, *Silene acaulis* grows in a very different climatic regime. Through proximity to the ocean and under the influence of the Japanese current, the climate is strongly maritime, very mild for the latitude, equable with almost continual cloud or fog and a great deal of fine mist. The frost-free season lasts 150 days and winter differs comparatively little from summer. The lowest temperature ever recorded is near zero F.

Observations by the author indicate that in this climate *Silene acaulis* grows on fellfields very much as it does on Trail Ridge.

Mt. Washington again offers different conditions than either of the stations described above. It is nothing much of a mountain. Its summit at 6,288 feet (2,000 m.) stands a thousand feet (300 m.) lower than the town of Estes Park at the foot of the Front Range. Yet the alpine zone above timberline supports one of the most remarkable assemblages of arctic-alpine plants in the world.

Despite its insignificant altitude, Mt. Washington has one of the worst of climates. The highest wind ever measured anywhere was recorded at the Mt. Washington Observatory. For weeks at a time in winter it blows a continuous hurricane never dropping down to 75 m.p.h. Even the summer winds approach hurricane violence.

Timberline trees on Mt. Washington bear clear testimony to the severity of conditions there. In contrast to the semi-prostrate trees of Trail Ridge timberline, those (spruce and fir) on the windiest places on Mt. Washington are held flat to the ground in close carpets which over considerable areas have the aspect of well-kept lawns. Extensive areas of such close carpets occur at an altitude as low as 4,100 feet (1,250 m.). (See Griggs 1946, Figs. 3, 4.)

On Ellesmere, the most northerly of the large islands of the Arctic Archipelago, *Silene acaulis* is "almost ubiquitous, occurring on practically all types of soil" where it "generally flowers and fruits freely," Polunin (1940: 180). Ellesmere has a climate more severe than any other place on earth except on the ice caps where no plants can grow. There is hardly ever a month without frost. But the few hardy species that live there manage to continue growth between the frequent freezes. It is recorded that another of them, *Saxifraga oppositifolia* had green buds in February, the dead of winter (Polunin 1948: 11). The scanty precipitation at all seasons is largely snow. Throughout the Arctic, precipitation is 10 inches (25 cm.) or less—an amount that everywhere produces a desert. But in north Ellesmere and north Greenland, it is only 5 inches (12.5 cm.). Speaking of this country in his great Survey of the Arctic Archipelago, Simmons (1913: 31) says, "The prominent and important factor I take its extreme dryness to be." Climatically, the cold dry High Arctic is thus about as great a contrast to the warm moist Alaskan coast as can be imagined. Yet a number of species in addition to *Silene acaulis* occur in both places.

High latitude arctic habitats moreover differ widely from southern alpine habitats in another factor of great importance to plants, *viz.* in the length of the periods of daily illumination. As is well known the seasonal sequence of flowering and fruiting is generally controlled by photoperiodic responses. It needs scarcely to be pointed out that there is an enormous difference bteween the continuous daylight of the north Ellesmere summer and the alternating daylight and darkness of Colorado. So far as I am aware no one has made extensive experimental comparison of the photoperiodic reactions of high arctic and high alpine representatives of wide ranging species like *Silene acaulis,* although the work of Clausen, Keck, and Hiesey and others approaches such an undertaking. Until that is done arctic- alpine ecology can have no very secure foundation.

II. *Arenaria obtusiloba*

Arenaria obtusiloba is an American arctic-alpine species ranging from "Labrador to Alaska south to New Mexico and California." It is allied to and "May not be distinct from *A. sajanensis*" (Harrington 1954: 234). The latter is "probably circumpolar or at least circumboreal" (Polunin 1940), goes as far north as Spitzbergen, comes down to Mt. Albert, Gaspé, and in the Rocky Mountains to Arizona. The taxonomy of the numerous Colorado Arenarias is, however, uncertain and confused. I simply follow local usage in calling my plant *A. obtusiloba.*

Arenaria obtusiloba grows in the same habitats as *Silene acaulis* and the two are nearly equivalent ecologically. When the cushions of neighboring plants of these two, growing radially, come into contact as often happens, they usually form a straight line junction. That is, both have the same vigor of growth and neither has any advantage.

Sometimes, however, the line joining intersecting cushions of the two species is slightly bowed outward, sometimes by stronger growth of *Silene,* sometimes the reverse, by *Arenaria.*

On bare ground where there is no competition, *Arenaria* grows faster than *Silene* and its mat reaches a larger size exceeding 24 inches (60 cm.). But its growth is looser—more like a mat than a cushion. Though starting from a tap root it puts out new roots almost anywhere. This is an important factor in its attainment of a larger size.

As might be expected, the list of plants which invade *Arenaria obtusiloba* is very much the same as that for *Silene*. It includes the following 22 species:

Silene acaulis
Salix sp.
Paronychia pulvinata
Eritrichium elongatum
Androsace septentrionalis subumbellata
Trifolium nanum
Trifolium dasyphyllum T. and G.
Lloydia serotina (L.) Sw.
Phlox caespitosa (by runners)
Festuca ovina brachyphylla
Luzula spicata
Trisetum spicatum (L.) Richt.
Sedum stenopetalum (by runners)
Sedum rosea (L.) Scop. (by runners)
Draba aurea
Haplopappus pygmaeus
Hymenoxys grandiflora
Artemisia scopulorum
Geum rossii
Polygonum bistortoides
Ranunculus adoneus Gray
Carex sp.

III. *Paronychia pulvinata*
(Figs. 2, 3, 4)

The tight cushion of *Paronychia pulvinata* differs almost as much and in much the same way from its relatives as does *Silene acaulis* from the numerous "catchfly" species of that genus. But *Paronychia pulvinata,* far from being cosmopolitan, is endemic to the central Rocky Mountains from Colorado to Wyoming and Utah. Although possessing much the same adaptations as *Silene acaulis* and occurring like that species chiefly on the fellfield, it is nothing like so common or so aggressive a colonist as *Silene.* This, notwithstanding the fact that seedlings of *Paronychia* can invade *Silene* and increase at the expense of strong cushions of that species.

Without having dug up enough representatives of *Paronychia* to make sure, I have the impression

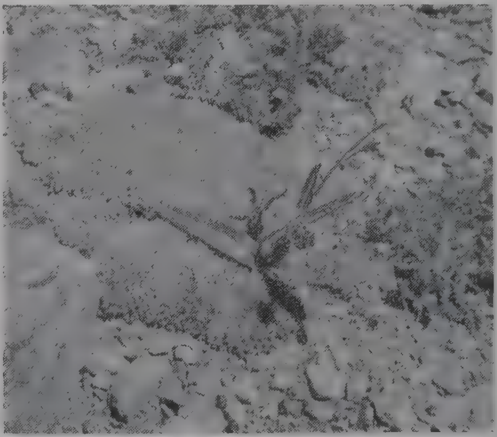

FIG. 2. *Paronychia pulvinata* invaded by *Polygonum bistortoides.* The bistort has a much thickened root, longer and deeper than its host (Fig. 3). Here it is thoroughly established. The *Paronychia* cushion measured about 5 x 8 inches. Above and at right, at "1 o'clock and 3 o'clock," *Geum rossii;* at 2 o'clock, *Arenaria obtusiloba* in flower.

that its root system is neither so strong nor so extensive as in *Silene*. Certainly its roots do not compare in strength with those of *Trifolium nanum* (Figs. 3, 5).

In my experience, *Paronychia* is common in some rather small areas, not generally distributed like *Silene*. Possibly it may have some rather special soil requirement.

Paronychia pulvinata invades *Silene acaulis* and *Arenaria obtusiloba*. It was seen invaded by the following 10 species:

Androsace septentrionalis subumbellata
Trifolium nanum (Fig. 4)
Eritrichium elongatum
Luzula spicata
Festuca ovina brachyphylla
Polygonum bistortoides
Arenaria fendleri Gray
Haplopappus pygmaeus
Dryas octopetala L. (once)
Geum rossii

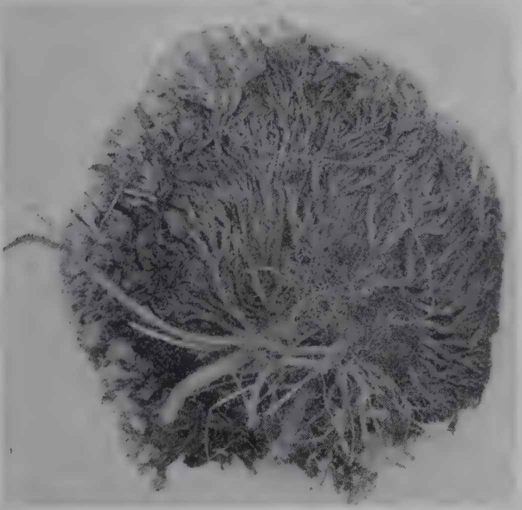

FIG. 3. The under side of a cushion of *Paronychia*, similar to that shown in Fig. 2. The radiating branches are in almost continuous contact. The seedling of any invader like those in Figs. 2 or 4 must be able to push its way through this dense matted growth. The cushion measured about 6.5 inches.

IV. *Trifolium nanum*
(Figs. 4, 5, 6, 7)

Trifolium nanum is one of three remarkable clovers endemic to the central Rocky Mountains, this one from Montana south to New Mexico and Utah. Like *Silene acaulis* and *Paronychia pulvinata*, it is so different from its allies that its relationship might not be recognized at first yet it has trifoliate leaves and the individual flowers have the form of clover blossoms though they are overlarge for the genus and instead of clustering in many-flowered heads are almost solitary, only one or two to a peduncle.

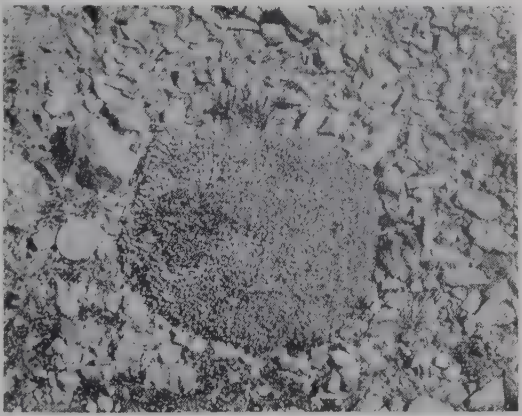

FIG. 4. *Paronychia pulvinata*, gray-green, invaded by *Trifolium nanum*, deep green. On the original Kodachrome, the yellow-green sessile flowers of *Paronychia* are conspicuous. They may still be made out on the black and white print. The invader was several years old but had not yet flowered. The 25 cent piece gives the scale. The cushion is about 6 inches in diameter.

Trifolium nanum forms a dense, thicker, more extreme type of cushion than those previously discussed. It may reach a large size. One was measured 15 x 20 inches (40 x 50 cm.).

It is supported by a much stronger root system the main trunks of which are two or three times as thick as in *Silene* (Fig. 4). Probably the ratio of roots to foliage is considerably higher than in *Silene* for many long feeding roots come off the tap roots. There are only a few fanshaped nodules. In its large root system may very well lie the explanation of the fact that *Trifolium nanum* is one of the most aggressive invaders of the cushions of other fellfield plants.

Within the tussocks of its hosts one may observe all stages in its growth. One little plant of *T. nanum* was observed in the middle of a strong cushion of *Silene*. It had two small leaves in June but by August had grown two more. By the end of the summer it had six leaves. The *Silene* stood alone on the gravel of the fellfield. No other clover plants were near it. In another case, a small clover plant growing in a cushion of *Silene* had five leaves this season: the first two were minute, the third quite small, the other two still only about one-fifth the normal size. The first two were already yellow and dying. This might appear to be the foliage of a very young seedling. But below the leaves described were the remains of two others presumably from the preceding year. And there was a strong thick tap root three inches (7.5 cm.) long with fine fibrous branch roots at the base. I could not well guess how old this "seedling" may have been.

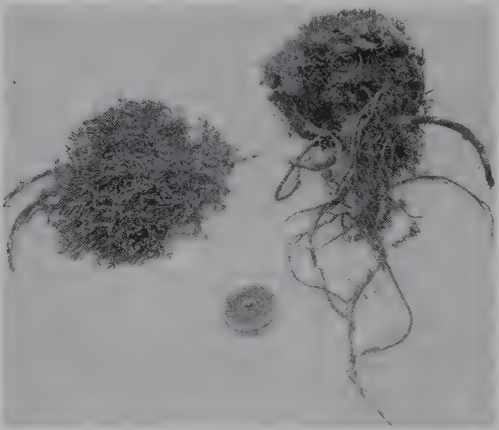

FIG. 5. Cushions of *Trifolium nanum* in top and side views. The pink flowers are only slightly brighter in the black and white print than the deep green leaves. The roots, broken off, are much stronger than in any other cushion plant observed and go far toward accounting for the dominance of this species in fellfields with especially strong wind exposure. The tape measure shown is 2 inches in diameter.

The expansion of the invading clover seems to be inexorable but it is very slow. Two or three decades are probably required for the development of a cushion 8-10 inches (20-25 cm.) in diameter. Figure 4 shows a comparatively early stage of invasion. The host was in full bloom but the invader had not yet flowered. Often, however, the clover will flower while it is still only a small rosette. For a number of years both host and invader flower freely together.

In most cases, no evident damage is done the host beyond the obvious loss of ground to the intruder. But sometimes examination reveals stems of the invader closely twined about the yellowed dying branches of its host which it was strangling.

Altogether it is not hard to see why *Trifolium nanum* is one of the most successful of the fellfield species. In some of the most exposed situations tussocks of this clover make up well over two-thirds of the vegetation. But only on the fellfield does it attain such abundance for its tussocks do not enter the grassy tundra extensively, and are not so sharply delimited as on the fellfield.

Closer analysis of the relations of invader and host than available time has yet permitted 1 would probably give a worthwhile insight into their competitive capacities, especially in *Trifolium nanum*. For example, a little grass (*Poa*) was found tightly wedged into the cushion of the clover. It had only two small leaves, shorter than those of the clover but there was a tiny inflorescence sticking up an inch above the surface of the cushion. It would certaily be rewarding to follow the history of such an invader over a series of years. And for this kind of study, Trail Ridge with its easy accessibility offers exceptional opportunity.

More than any other species *Trifolium nanum* has roles as both invader and as host to species as listed below:

Trifolium nanum invades:
Silene acaulis
Arenaria obtusiloba
Paronychia pulvinata

The following 21 species were observed invading *Trifolium nanum:*
Arenaria fendleri
Sedum stenopetalum (by runners)
Trisetum spicatum
Luzula spicata
Poa sp.
Artemisia scopulorum
Mertensia viridis (by runners)
Draba aurea
Eritrichium elongatum
Primula angustifolium
Androsace septentrionalis subumbellata
Agropyron scribneri Vasey
Haplopappus pygmaeus (by seed and by runners)
Trifolium parryi Gray (by runners)
Castilleja occidentalis (by seed)
Lloydia serotina
Erysimum asperum (Nutt.) DC.
Ranunculus adoneus
Polygonum bistortoides
Carex spp.
Geum rossii

The competitive relations between invader and host are naturally clearest when the host forms a tight compact cushion. Then a germinating seedling from the beginning enters a vigorous struggle for existence as it pushes into its host. When the body of the host is looser, a mat rather than a cushion, a germinating seed may find space and soil enough between the branches of the mat to become established before it comes into direct physical contact or root competition with its host. In such situations, it is not possible to assess so exactly the comparative capacity of the two species for dominance as it is between two dense cushions like *Paronychia pulvinata* and *Trifolium nanum*.

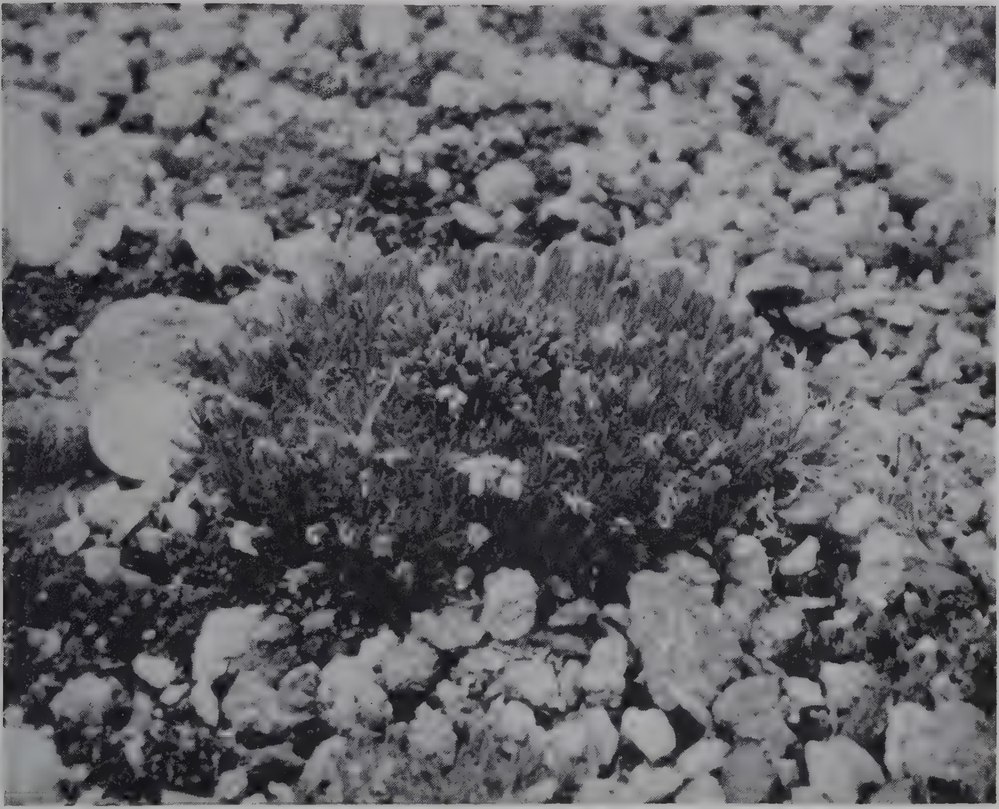

FIG. 6. *Trifolium nanum* invading *Silene acaulis.* The trifoliate clover, past blossoming, has obviously increased at the expense of its host. The 25 cent piece gives the scale.

V. *Trifolium dasyphyllum*

The second of the three endemic clovers, *Trifolium dasyphyllum,* is not so characteristic of partly bare fellfields as of areas transitional between fellfield and closed grassy tundra. Its internodes are longer than in *T. nanum* and it usually forms loose mats rather than tight cushions. Sometimes however it grows more slowly and completely occupies the ground. That is to say, *T. dasyphyllum* is a transitional species. Seedlings starting between the branches of a loose mat cannot rightly be classed as invaders. But those listed below were found coming into tight mats of the clover and were adjudged comparable with the invaders listed under the preceding species.

Trifolium dasyphyllum was seen invading:

Arenaria obtusiloba

The following 7 species were observed invading it:

Trisetum spicatum
Arenaria fendleri
Sedum stenopetalum
Draba aurea
Polemonium confertum Gray
Hymenoxys grandiflora
Geum rossii

Trifolium parryi, the third of the endemic clovers, has long subterranean runners by which it spreads rapidly into established vegetation of many kinds. Although this clover does not grow on the open fellfield, the most vigorous young plants do start on bare spots rather than on the closed tundra.

Invasion by runners is obviously in a different class from that of seedlings. A seedling with no resources beyond the food carried in the seed must be definitely superior to its host in some such way as a parasite which must possess a higher osmotic pressure than its host in order to push into its tissues. But a runner reaching in from a plant securely established outside the point of invasion may be backed by the total photosynthetic capacity of a well-established plant. *Trifolium parryi* sometimes sends its runners into vigorous clumps of species high up toward the climax, *e.g., Carex scopulorum* and *Geum rossii.*

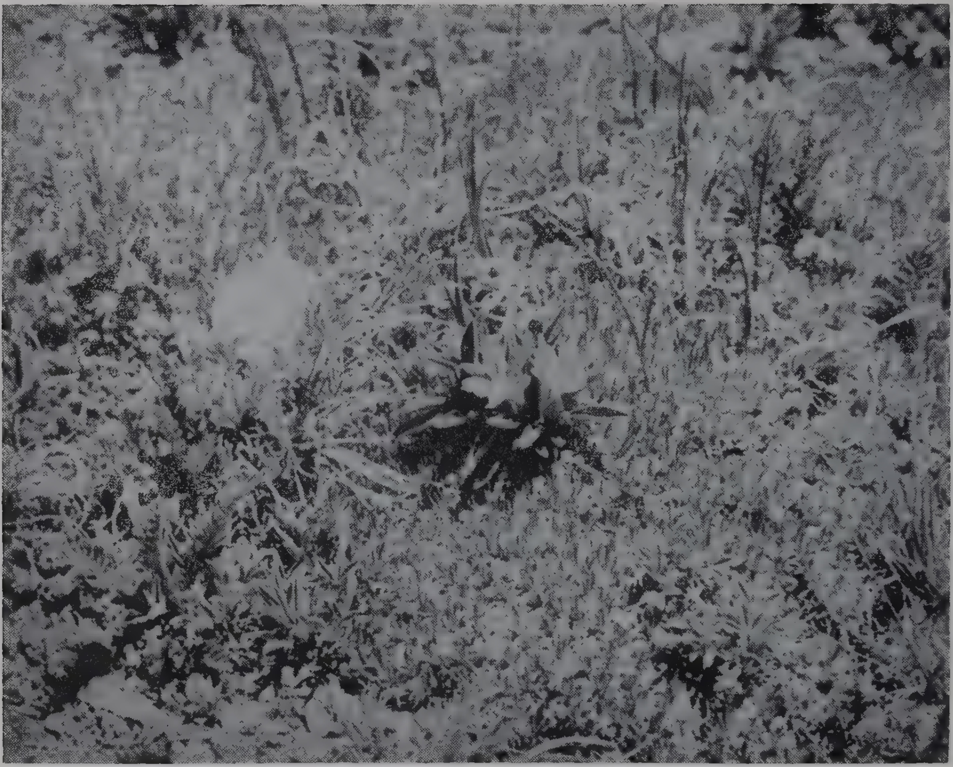

FIG. 7. *Primula angustifolia* (flowering) and young *Trifolium nanum* (at 7 o'clock) invading a cushion of *Silene acaulis.* The erect pairs of parallel veined leaves beside and behind the primrose are *Lloydia serotina,* some of them also invading the *Silene* cushion.

DISCUSSION

But invasion by runners cannot yet be tied into the succession as a whole. I am hoping that it may be possible to continue studies further into the "grassy" tundra where the dominants are turf formers in contrast to the isolated cushion plants of the fellfield.

The most significant feature of the invasion of the cushion plants is the fact already mentioned that they practically always go the same way, never the reverse. In the hundreds of cases of invasion observed, except once or twice, an invading species was never seen to be invaded by its host.

Thus, it is possible to arrange these species in the order of their comparative capacity for dominance. They form what might be called, figuratively, a competitive ladder, as follows:

Tentative competitive ladder on the tundra

37. *Kobresia bellardii* (All.) Degl.
36. *Geum rossii*
35. *Hymenoxys grandiflora*
34. *Polemonium confertum*
33. *Castilleja occidentalis*
32. *Carex* spp. (sterile)
31. *Carex scopulorum*
30. *Trifolium parryi*
29. *Erigeron* spp.
28. *Mertensia viridis*
27. *Draba aurea*
26. *Lloydia serotina*
25. *Haplopappus pygmaeus* (Fig. 8)
24. *Artemisia scopulorum*
23. *Trisetum spicatum*
22. *Luzula spicata*
21. *Poa* spp.
20. *Agropyron scribneri*
19. *Festuca ovina brachyphylla*
18. *Sedum stenopetalum*
17. *Selaginella densa* Rydb.
16. *Eritrichium elongatum* (Fig. 9)
15. *Trifolium dasyphyllum*
14. *Trifolium nanum* (Figs. 4, 5, 6, 7)
13. *Polygonum bistortoides* (Fig. 2)

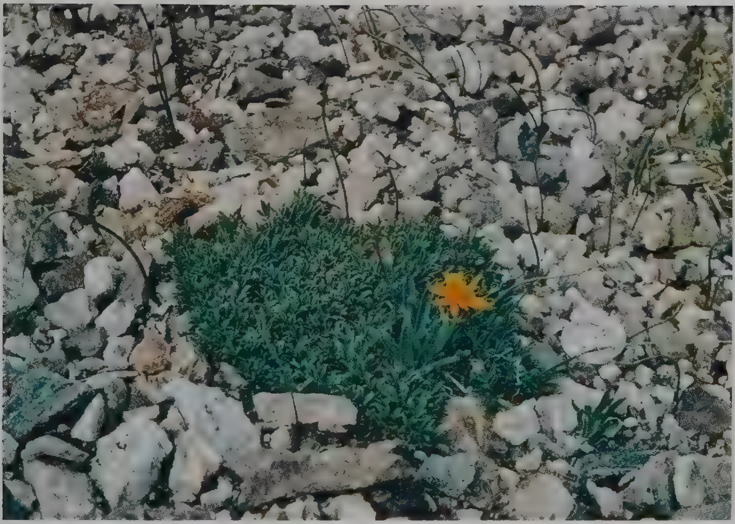

FIG. 8. *Haplopappus pygmaeus* invading *Trifolium nanum.* The vertical oblong leaves of the invader contrast with the trifoliate leaves of the host. The clover tussock measures 4.5 inches.

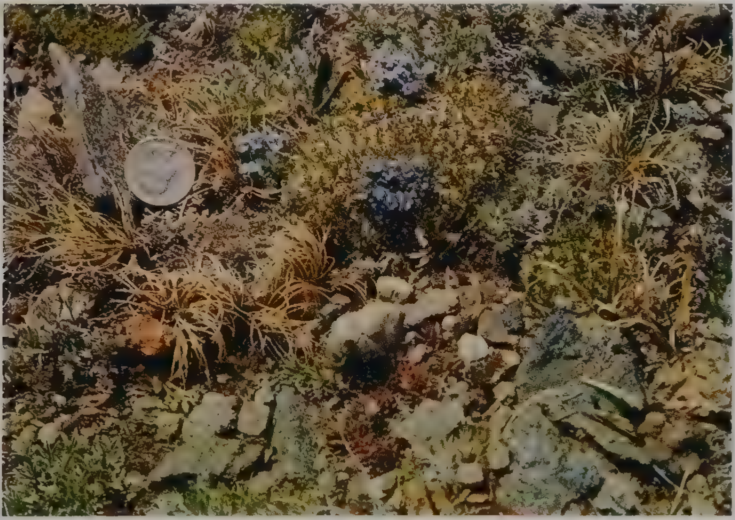

FIG. 9. Forget-me-not, *Eritrichium elongatum,* invading a cushion of *Silene acaulis* which is just coming out of the winter condition, June 28. The two other plants of *Eritrichium* in the field demonstrate that seeding is random. Since both are rooted in the ground, they show that colonization by new plants is by no means limited to the invasion of established cushions of older plants.

12. *Polygonum viviparum*
11. *Arenaria fendleri*
10. *Androsace septentrionalis subumbellata*
9. *Paronychia pulverulenta*
8. *Draba fladnizensis*
7. *Cerastium* sp. cf. *beeringianum*
6. *Arenaria rubella*
5. *Primula angustifolia*
4. *Salix* sp.
3. *Arenaria obtusiloba*
2. *Silene acaulis*
1. *Saxifraga flagellaris* Willd.

I would in the first place emphasize the word *tentative* in my heading for the competitive ladder. I list the species named in the order given because I believe it is clear that we have here an opportunity and a method for discovering the relative dominance of the species of the fellfield—not that I think the order of dominance is as yet correctly established.

The anchor points in the ladder are of course the dense cushion plants that are much invaded. Where these, like *Paronychia* and *Trifolium nanum,* are invaders as well as invaded at different levels, their place on the ladder is definitely fixed. But we do not yet have criteria for assessing the relative dominance of species which invade the same host but whose contacts with each other have not yet been sufficiently studied.

The rate of growth of the invaders in some cases seems to be retarded as compared with seedlings starting in the open ground. In and around one tussock of *Silene* for example were half a dozen rosettes of *Erysimum asperum,* three in the ground and three invading the *Silene*. Early in the season, all appeared to be of the same age and vigor. Two of those rooted away from the *Silene* blossomed but none of those in the host flowered. Enough of this sort of thing to prove the point was not seen. And in some cases the invaders seemed to grow with a vigor equal to plants rooted directly in soil. But in other cases like *Draba crassifolia* mentioned below the invader is definitely short-lived.

I started this paper by pointing out that the struggle for existence on the tundra in most places is too complex for analysis. Now that some of the simpler cases where one species invades one other have been presented, I would caution the reader against over-simplification. Possibilities of error are presented by every case met with.

When two species grow together which one is increasing at the expense of the other? It makes a difference whether the "invader" occupies the center of the host's cushion or the periphery. If it is at the center its roots must come into direct conflict with the tap root of its host. If the invader is marginal it might have been established first and it might be the "host" which has surrounded the "invader" by strong radial growth. Because of this possibility I have listed as invaders only plants that occupy a position well in from the margin of the host cushion.

There are other means of ascertaining which plant of a pair is the aggressor. Looking simply at a rosette of sunflower, *Hymenoxys grandiflora* in the edge of a *Silene* tussock one might conclude that *Silene* had engulfed the sunflower. But *Silene* is a long lived, slow-growing perennial and the sunflower is a monocarpic plant flowering only once and then dying like a biennial. Without doubt the sunflower is the younger of the two and is the invader.

When both members of a pair are long-lived perennials their relative age becomes a significant index. If both have been long established, it is often impossible to unravel the history of their association. But when one is a small seedling coming out of the center of the other and there are no plants of the species nearby to send runners into the host, doubts are resolved. Small seedlings are difficult to photograph effectively but I refer back to the little seedling tentatively identified as *Mertensia viridis* reported under *Silene* and to the small plants of *Trifolium nanum* also in well-developed cushions of *Silene* described under *Trifolium nanum*. The location of some such pairs have been definitely described so that they can be found again and their history followed in subsequent years.

Rank in what I have called the competitive ladder is not, however, the same as rank in the succession. *Silene acaulis* does indeed appear as the lowest member of both. But while the capacity of one species to invade the cushions of another involves some sort of superior growth potential, a high place in the succession involves a capacity for holding on and continuing growth over a period of years—which is something else. Two examples will make the point clear. Diminutive *Draba crassifolia* which is scarcely an inch tall was thrice seen invading *Silene acaulis*. Its yellow flowers just reached the surface of the *Silene* cushion. But its leaves which are all in a basal rosette, were invisible in the dense foliage of its host, overshaded and thus cut off from the light necessary for photosynthesis. This invader is, in our area, an annual or perhaps biennial ephemeral which never grows enough to displace its perennial host.

Seedlings of the snow buttercup, *Ranunculus adoneus,* invade the mats of many species, some of them high in the succession, *e.g., Geum rossii* and

Artemisia scopulorum, both of which are constant constituents of grassy closed tundra. The *Ranunculus adoneus* comes to flower within tight masses of these and other species yet it persists there only briefly. Optimum development of the snow buttercup occurs only on nearly bare muddy ground kept wet late in the season by melting snow. It is as low in the succession as the two hosts mentioned are high.

So far as I am aware no such pattern of invasions involving other hosts than *Silene acaulis* has been reported in other arctic-alpine regions. Why not? Is it that nothing analagous occurs in other regions? It is my hope that other tundras will be examined from this point of view and compared with Trail Ridge. Without undertaking a prediction I should be inclined to expect that it will be found that the pattern differs elsewhere. And if the order of dominance turns out to be different in different regions where the same species occur, that would give us a precise means for comparative description of different tundras. Then, with detailed comparisons in hand we could begin to look hopefully toward the discovery of the factors responsible for the diversity. If on the other hand it should turn out that the pattern of competition on fellfields of the Front Range of the Rocky Mountains obtains generally, then in view of the diverse climates in which some arctic-alpine species are indigenous, serious doubts of the pertinence of the climatic data customarily included in ecological literature would be raised. Such questions have in fact long plagued students of the ecologoy of wide-ranging species. The matter can be finally settled only by such transplant and controlled condition experiments as those initiated by Harvey Monroe Hall and carried forward by Clausen, Keck, and Hiesey (1948) in California. Meanwhile close comparisons of competitive patterns in similar but distant tundras can greatly elucidate this complex problem.

Summary

Wide-ranging arctic-alpine plants like *Silene acaulis* inhabit regions with very diverse climates. Are these taxonomic units also ecologic units?

In Rocky Mountain National Park, seedlings of many tundra plants invade the cushions of fellfield species.

Thirty-three species were observed to invade *Silene acaulis;* 22 were seen invading *Arenaria obtusiloba;* 10 invaded cushions of *Paronychia pulvinata;* 21, *Trifolium nanum;* 7, *Trifolium dasyphyllum;* and this list including 93 invader-host pairs is by no means complete. A large majority of these 93 pairs have been observed repeatedly, many times over.

The invasions follow a regular pattern from which the relative dominance of the species concerned can be determined. On this basis a tentative competitive ladder for some of the tundra species is set up.

Is there a similar pattern of invasion and succession in other arctic-alpine regions? Or do the diverse arctic-alpine climates produce radically different patterns of succession? Similar determinations of the order of dominance in other arctic-alpine regions can answer the questions posed and permit the establishment of a comparative arctic-alpine ecology which hitherto has been beyond our reach.

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A STUDY OF MUTUAL OCCURRENCE OF PLANT SPECIES[1]

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The floristic basis of community classification, both European and American, is dependent upon the fact that certain species tend to occur together. Efforts to determine degree of mutual occurrence have led to the development of objective, quantitative methods which are based upon the recognition of three major spatial levels of biotic relationship: (1) geographic, (2) communal, and (3) interspecific.

On the first level, evolutionary and historic factors determine the geographic distribution of species and their mutual occurrence within the same geographic area. The second level considers, within a common geographic area, the interaction of species with the community as a whole. Joint occurrence on this level is determined by the ability of species to enter the community and to survive in it by successfully meeting the conditions which are present as the result of interaction between the community and its external environment. Mutual community occurrence has usually been sampled within stands whose areal extent is limited only by the criterion of homogeneity.

The third level is that of the direction reaction within communities of species with each other. On this level, species have been considered to be either more or less indifferent, with their mutual occurrences determined by chance juxtaposition, or to be not at all indifferent with an active attraction or repulsion of members of their own or other species. Most of these direct reactions take place within relatively small areas and can only be discovered, for herbs and shrubs, with the use of quadrats of less than a few square meters in size.

Measurements of community similarity on the basis of the total species composition have been extensively utilized since the development of the first coefficient of community by Jaccard (1902). These measurements, which include the papers of Gleason (1920), Kulczyński (1927), Katz (1930), Sörenson (1948), Motyka, *et al.* (1950), Odum (1950), Webb (1950), Whittaker (1952), Culberson (1955), and Hanson (1955), have attempted to order stands by a consideration of qualitative or quantitative similarity of species composition.

The basic formula for a quantitative coefficient of community was first presented by Gleason (1920) as a modification of Jaccard's index. The same quantitative coefficient has later been independently proposed by Sörenson (1948), Motyka, *et al.* (1950), Odum (1950), and others.

Measurements of individual interspecific association have been proposed or discussed by Forbes (1925), Dice (1948), Cole (1949), Nash (1950), and Goodall (1952), and have been used in phytosociologic studies by Gilbert and Curtis (1953), Goodall (1953), de Vries (1953), and Hale (1955).

Both the methods of the measurement of similarity of community composition and of individual interspecific association have been proposed as techniques to relate species to each other and to determine similar groups, if any. The present study will compare these two approaches and will attempt to point out the limitations in their usage.

METHODS

To make certain that a field study includes variations in species behavior on both the community and individual level, it is necessary to sample an area with a wide diversity in community composition, such as is shown by one in which the species at one end of gradient do no occur at the opposite end. The vegetation of Trempealeau Mountain, Perrot State Park, Wisconsin (T 18N, R 9W, S 19, NW-SE 1/4 and 44° 01′ N, 91° 30′ W) meets such a criterion. Around the side of the cone-shaped hill, from north-east through south to west, there is a change in amount of sunlight and in exposure to southwesterly drying winds, which is accompanied by a change in vegetation from closed-canopied forest through oak opening and then into prairie. The area was sampled during the third week of August, 1952, and at that time it gave no evidence of recent disturbance, either of cutting or grazing. It is protected from intrusion by being almost surrounded by the Mississippi River.

In sampling the stand for the occurrence of herbs and shrubs, a belt 400 m. long, of 40 contiguous plots each 10 m. on a side, was laid at a constant elevation around the hill in an area which

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[1] This work was supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation. The author wishes to thank Dr. J. T. Curtis for his advice in the preparation of the manuscript.

had a fairly even degree of slope and which promised to give a uniform transition from forest to prairie. Each plot, therefore, contained 100 sq. m. an area considered to be larger than the area of biotic influence of the individual grasses, forbs, and small growing shrubs which were likely to be found. Within each 100 sq. m. plot, 5 herb and shrub quadrats, each one m. on a side, were laid at random, making a total of 200 small quadrats for the study. Presence of species was recorded for each quadrat. The choice of a one-meter quadrat, though possibly of too great a size to measure some individual interspecific biotic reactions, was chosen as a compromise size. A detailed study of specific interrelationships would presumably need a graduated set of quadrats with sizes determined by the area of individual influence. Environmental measurements were also taken; the measurement of light is relevant to the present study. Four light intensity readings were taken with a Weston Photometer on the 4 quarters of the first 2 herb quadrats of each plot. The readings were taken around noon on clear days when the sun was directly facing the slope of each plot.

In addition to the Trempealeau sampling, a similar study was made of a transition from dry lime prairie into oak opening on Butte de le Chien (T 6N, R 6W, S 23, NW:NW 1/4 and 43° 58′ N, 91° 04′ W) which overlooks the Wisconsin River near Wyalusing State Park. The sampling of Butte de le Chien was also based upon contiguous plots laid along a transect which moved from prairie into forest. Five stand segments, each containing four 10 x 10 m. plots were sampled with a measurement of species presence within 1 x 1 m. quadrats. Five 1 x 1 m. quadrats were laid in each of the 20 plots making a total of 100 quadrats.

RESULTS

Community similarity

The first ordering of the Trempealeau plots was accomplished by use of the technique of the assignment of adaptation values (Curtis and McIntosh 1951). The average adaptation value of the common species was calculated for each of the 40 plots by the method given below. These common species were the 16 most frequent in the 200 herb quadrats; they accounted for a sum of frequency of 897 out of a total sum of frequency of 1674. The 5 herb quadrats of each plot had an adequate representation of these species.

The objective assignment of adaptation values was accomplished by use of an index of amplitudinal correspondence. This index was determined by dividing the number of plots of joint occurrence of the two species (Sj) by the average number of plots of occurrence of the two species, a and b; $\frac{\text{Sa} + \text{Sb}}{2}$. The index then can be expressed as: $C = \frac{\text{Sj}}{\frac{\text{Sa} + \text{Sb}}{2}}$, which simplified to:

$$C = \frac{2\,\text{Sj}}{\text{Sa} + \text{Sb}}.$$

This index was calculated for the 16 most frequent species. Their matrix is presented in the lower left of Table I. The species in Table I and succeeding tables follow the nomenclature of Glea-

TABLE I. Indexes of amplitudinal correspondence—Trempealeau*

	Osmunda	*Aralia*	*Eupatorium*	*Geranium*	*Desmodium*	*Carex*	*Galium*	*Celastrus*	*Solidago*	*Amphicarpa*	*Euphorbia*	*Monarda*	*Amorpha*	*Andropogon*	*Coreopsis*	*Rosa*
Osmunda c.																
Aralia n.	66															
Eupatorium r.	18	70														
Geranium r.	33	63	56													
Desmodium g.	40	65	55	72												
Carex p.	26	68	68	67	69											
Galium b.	12	52	60	59	57	60										
Celastrus s.	24	50	52	69	70	69	81									
Solidago u.	18	55	54	65	76	72	86	84								
Amphicarpa b.	14	52	59	62	74	74	81	85	92							
Euphorbia c.	00	26	43	43	54	52	70	71	81	82						
Monarda f.	00	23	32	45	57	45	69	70	77	78	83					
Amorpha c.	00	31	37	41	40	43	72	69	69	66	74	58				
Andropogon g.	00	19	22	51	50	46	66	72	75	76	85	80	75			
Coreopsis p.	00	05	13	27	38	32	57	59	60	61	72	71	64	68		
Rosa a.	00	00	00	26	37	31	51	57	62	64	76	63	75	82	80	

*The left-lower half of the table shows the indexes of amplitudinal correspondence of the species. These indexes measure the relative joint occurrence of the species among plots and give an approximate representation of their nearness along a phytosociologic gradient.

son (1952). *Antennaria* sp. represents plants which have uniform characters throughout the Trempealeau study area, but whose taxonomy is awaiting treatment of all Wisconsin species.

The species in Table I were arranged by inspection into an order which had as end-points *Osmunda claytoniana* and *Rosa arkansana.* These species were considered to be the greatest relative distance apart on the basis of the facts that they never occurred together in the same plot, and that they occurred less often with other species placed at opposite ends of the arrangement. *Osmunda,* for example, did not occur in any of the plots which contained *Coreopsis palmata* and *Andropogon gerardi* which is not the case for *Osmunda's* nearest neighbor, *Aralia nudicaulis.*

The patterns of species interchange in Table I are fairly evident. It can be seen that the indexes of amplitudinal correspondence of *Rosa arkansana* and *Coreopsis palmata* more or less uniformly increase from the left to the right side of the table indicating that *Rosa* and *Coreopsis* are found increasingly with the species toward the right. The same pattern occurs but in a reverse direction for *Osmunda claytoniana* and *Aralia nudicaulis,* while plants found toward the middle of the table, such as *Celastrus scandens* and *Solidago ulmifolia,* are more closely allied with the other species of the middle than with those of either of the ends. The order of species in Table I was used to assign adaptation values. The first 5 species were given a value of 1, the next 5 a value of 2, and the last 6 a value of 3. The frequencies of the species in each plot were then weighted by their respective adaptation values by the following formula:

$$\text{P. I.} = \frac{\Sigma\ (\text{Frequency of each species} \times \text{its adaptation value})}{\Sigma\ (\text{Frequency of each species})}$$

The plots were arranged in an order of the increasing magnitude of their plot index.

The arrangement of plots by the use of adaptation values is dependent upon the placement order of species in Table I. A second independent ordering of plots is, therefore, desirable. This ordering was achieved by the use of Gleason's modified coefficient of community (1920). In calculating a matrix of these coefficients, the number of plots was reduced to 20 by a consideration of every other plot. The matrix contained, therefore, 190 values; it is presented in Table II.

The position of plots in Table II was arrived at by an inspection process, discussed by Motyka, *et al.* (1950), which attempted to place plots with higher coefficient values in a greater proximity to each other. The results are presented numerically in the left-lower half, and graphically in the right-upper half of Table II. The patterns of plot relationship show a smooth and continuous interchange of coefficient values.

The first and second Trempealeau plot ordinations were then compared with each other using a test for rank correlation (Snedecor 1946). The orders were found to be correlated at the one per cent level of significance.

Frequency distributions

The first Trempealeau ordination was divided into 5 equal segments and the per cent frequency of 48 species (all species which appeared in 5 or more herb quadrats) calculated for each of the segments. The resulting frequency distribution patterns are shown in Table III. The first column of Table III contains 9 plots; *Osmunda claytoniana* with a per cent frequency of 71.0 in the first column occurred, therefore, in 32 of its 45 herb quadrats. The number of plots in each size class is listed at the top of each column in Table III. The frequency distributions of the 32 less frequent species in Table III have the same patterns of increase and decrease shown by the 16 more frequent species which were used in making the plot ordination. The nature and interpretation of the 48 amplitude patterns will be given in the discussion.

Interspecific association

The basis of interspecific association is that if species are indifferent to each other (*i.e.,* independent), they will occur together more or less by chance, while if they are not indifferent (*i.e.,* dependent), they will occur together more often or less often than can be expected by chance. Since the arrival and survival of species within a community is largely the result of interaction between the species and the community as a whole, then whether or not two species occur together in the same stands does not depend, except in the case of mutualism or parasitism, upon their degree of direct biotic relationship and should not influence its measurement. If stands are included in the study in which only one or neither of the species occurs, then an index of interspecific association does not measure individual biotic interaction alone, but also includes degree of mutual community occurrence (amplitudinal correspondence) which cannot be determined by an index based upon expected random joint occurrence. The calculation of interspecific association, if it is to measure only individual biotic reaction, should, therefore, be

TABLE II. Coefficients of community—Trempealeau

Stand	9	7	17	19	1	11	5	15	3	13	37	39	29	31	21	33	27	23	35	25
9		●●	○○	••		••														
7	48		○○	○○	••	••	••													
17	36	33		○○	○○	●●	○○	○○	••	••	••	••	••		••					
19	29	39	43		●●	●●	••	○○	••	●●	••	••	••	••	••	••				
1	13	26	33	47		●●	●●	○○	○○	○○	••	••	••		••					
11	23	28	46	61	47		○○	●●	○○	○○	••	○○			••	••		••		
5	08	20	36	26	53	39		○○	○○	○○	••	••			••		••		••	
15	14	11	41	42	40	59	45		○○	●●	○○	●●	••	••	○○	••	••	••	••	
3	05	12	24	20	45	39	38	42		●●	••	○○	••	••	○○		••	○○	••	
13	10	12	29	52	42	38	44	58	52		○○	●●	○○	••	○○	••	○○	○○	••	••
37	06	11	25	30	17	19	29	36	28	45		●●	●●	●●	●●	○○	○○	○○	○○	••
39	05	05	22	27	25	34	30	48	31	50	52		●●	••	○○	○○	○○	○○	●●	••
29	06	08	19	29	16	04	15	29	24	44	55	62		●●	○○	●●	●●	○○	○○	○○
31	05	04	15	20	10	11	14	22	23	30	49	30	46		○○	●●	○○	●●	○○	○○
21	04	06	19	30	24	28	24	43	36	45	50	41	40	37		●●	○○	●●	○○	○○
33	03	03	13	20	10	16	15	30	14	27	40	40	52	46	48		●●	○○	●●	○○
27	00	00	15	14	07	13	21	22	16	32	41	44	47	45	36	50		●●	○○	●●
23	00	00	11	12	14	16	15	29	33	43	40	36	43	46	50	40	50		●●	○○
35	00	00	11	14	05	11	17	24	17	30	41	40	32	40	32	47	42	57		○○
25	00	00	03	05	02	06	09	12	10	19	21	30	32	31	32	45	48	37	45	

*The left-lower half of the table shows the coefficient values for every other Trempealeau plot. The values are calculated from Gleason's modification of Jaccard's Coefficient of Community, and give the degree of vegetational similarity of each plot with every other plot. The arrangement of plots is based upon an attempt to place plots of a high similarity into a close proximity. Values above 45 indicate a very high similarity, while values of 00 indicate no similarity with no species in common. The right-upper half of the table is a schematic presentation of these values. All coefficients of from 00-15 are represented by an empty cell; those values from 16-30 by a pair of dots; those values from 31-45 by a pair of hollow circles; and those values from 46-62 by a pair of solid circles.

restricted to the quadrats of those stands or plots which contain both species. An illustration using the Trempealeau data can be given. If the association of *Osmunda claytoniana* and *Aralia nudicaulis* is measured on the entire 200 quadrats of the study, which includes many plots in which only one or neither of the species occur, the value, using Cole's index (Cole 1949), is +.27. If, by chance, the Trempealeau study had included another 200 quadrats in the prairie where neither *Osmunda* nor *Aralia* occur, then the increased number of quadrats would lead to a decreased expected joint occurrence and the association value increases to +.42. By merely lengthening the study area in a direction in which neither species occurs, their association value can be increased. A different situation arises if the study area is increased to include plots in which one of the species occurs but not the other. Then their expected joint occurrence is increased, their actual joint occurrence remains the same and their association value decreases.

The different interspecific association results which can be gained by using all quadrats or only those in stands or plots in which both species occur, are illustrated in Table IV. All values in Table IV and in Table V are determined by Cole's index (Cole 1949).

In the right-upper part of Table IV only quadrats in plots of mutual occurrence were considered in calculating the index values. These values show, after a check for significance with Chi-square, that the great majority of species combinations (79 of a total of 96 values) are independently associated. Only 4 values show a highly significant dependence of association. They are *Desmodium glutinosum* and *Andropogon gerardi,* which are negatively associated; *Galium boreale* and *Monarda fistulosa,* which are negatively associated; *Carex pensylvanica* and *Andropogon gerardi,* which are positively associated and *Geranium maculatum* and *Aralia nudicaulis,* which are also positively associated.

In the left-lower part of Table IV all quadrats were considered in calculating Cole's indexes. It can be seen that, to a large degree, the association index values reflect mutual occurrence on a plot level as measured by the indexes of amplitudinal correspondence of Table I. The values for *Rosa arkansana,* for example, uniformly increase from a low of —1.0 to a high of +.43. In general, species with a high correspondence, that is, those found together in the same plots, had medium to high positive association values. Those species with a moderate correspondence had association values around 0 and those with a low correspondence had association values of medium to high negative association. This partial determination of association value by degree of habitat preference as represented by mutual plot occurrence is considered to be an adequate reason for limiting the use of the indexes to stands or plots containing both species.

The measurement of interspecific association was also calculated for the 100 quadrats and 20 plots of the Butte de le Chien study and presented in Table V. In the lower-left part of the table, association is figured with all quadrats contribut-

Table III. An oak-opening herb and shrub ordination—Trempealeau*

Species — Column:	1	2	3	4	5
Number of Plots:	9	7	11	7	6
1. *Osmunda claytoniana*	71	03	—	—	—
2. *Solidago flexicaulis*	15	03		—	—
3. *Rubus allegheniensis*	31	23	02	—	—
4. *Aralia nudicaulis*	60	83	18	—	—
5. *Pteridium aquilinum*	15	28	07	—	—
6. *Smilacina racemosa*	13	14	11	—	—
7. *Eupatorium rugosum*	13	46	22	—	—
8. *Geranium maculatum*	31	37	38	03	03
9. *Desmodium glutinosum*	33	40	31	10	03
10. *Smilacina stellata*	02	06	05	—	—
11. *Diervilla lonicera*	04	37	24	—	—
12. *Cornus racemosa*	13	08	11	03	03
13. *Carex pensylvanica*	13	48	51	23	—
14. *Parthenocissus vitacea*	—	11	04	—	03
15. *Rhus radicans*	02	11	44	—	—
16. *Panicum latifolium*	02	11	04	10	03
17. *Aquilegia canadensis*	—	06	05	—	03
18. *Celastrus scandens*	13	51	49	23	31
19. *Galium boreale*	07	34	53	37	14
20. *Amphicarpa bracteata*	11	51	82	77	34
21. *Solidago ulmifolia*	20	54	67	57	46
22. *Vitis riparia*	04	03	14	23	-
23. *Ceanothus americanus*	—	—	20	10	—
24. *Comandra richardsiana*	—	03	13	13	11
25. *Helianthus strumosus*	02	14	27	56	34
26. *Monarda fistulosa*	—	11	31	37	46
27. *Thalictrum dioicum*	—	08	29	32	28
28. *Amorpha canescens*	—	08	13	37	34
29. *Apocynum androsaemifolium*	02	03	18	14	23
30. *Euphorbia corollata*	—	11	27	40	48
31. *Physocarpos opulifolius*	—	—	14	20	14
32. *Heliopsis helianthoides*	—	—	29	47	28
33. *Lithospermum canescens*	—	—	04	07	03
34. *Symphoricarpos occidentalis*	—	—	16	37	28
35. *Solidago rigida*	—	—	05	07	08
36. *Aster azureus*	—	—	04	17	08
37. *Anemone cylindrica*	—	—	02	10	03
38. *Andropogon gerardi*	—	06	22	43	68
39. *Solidago nemoralis*	—	—	05	07	11
40. *Antennaria* sp.	—	03	02	30	23
41. *Coreopsis palmata*	—	—	18	43	54
42. *Rosa arkansana*	—	03	14	70	77
43. *Petalostemum purpureum*	—	—	02	07	11
44. *Cassia fasiculata*	—	—	05	10	26
45. *Phlox pilosa*	—	—	05	07	23
46. *Potentilla arguta*	—	—	—	10	11
47. *Lespedeza capitata*	—	—	04	11	26
48. *Petalostemum candidum*	—	—	02	07	20

*This table shows the frequency distribution behavior of 48 species along the first Trempealeau plot ordination. The values represent per cent frequency of the species in the 1 x 1 meter quadrats of the plots of the five columns into which the ordination was divided. The ordination represents a phytosociologic alignment and not a spatial gradient as it exists in the field. In general, there is a smooth transition, through the oak-opening, from column 1 which is a more closed canopy forest to column 5 which is prairie.

ing to the expected value. In the upper-right of the table only the quadrats of those plots which contained both species were considered.

The Butte de le Chien interspecific association data show the same patterns as that of Trempealeau. The indexes determined by the entire 100 quadrats reflect mostly the change in species presence from prairie into oak opening, with species toward the left being prairie plants and those toward the right more common under open forest canopies. The actual association of the species in the upper-right of the table demonstrates, as does the Trempealeau data, that the large proportion of species is independently associated.

Within plots of mutual occurrence 4 pairs of species show a highly significant association. *Stipa spartea* is positively associated with *Amorpha canescens; Andropogon gerardi* is positively associated with *Amorpha canescens,* and with *Corylus americana,* while *Corylus americana* is negatively associated with *Amphicarpa bracteata.*

Discussion

The limitations and the complementarity of the two basic approaches to species mutuality (neglecting geographic considerations) presented in the introduction can be stated briefly. On the level of community behavior where stands or plots are to be ordered in objective classifications and species ecologic amplitudes are to be determined, the use of an index of interspecific association gives data which is difficult to interpret. When such an index is used, then, in general, the indexes of association will show species which have little amplitudinal overlap to have a negative association, species which have a moderate overlap to have an independent association, and species with a high overlap to have a positive association. The suggestion that interspecific association not be used to measure the ecologic amplitudes of species is, therefore, made for the following reasons: (1) there is no way to know to what degree the index reflects changes in community composition as opposed to the influence of direct species reactions, and (2) as previously demonstrated, the values of an association index are influenced by the length of the ecologic gradient and the number of samples.

A simple and easily workable index is suggested to measure the relative overlap of species amplitudes. These amplitudes can be measured among such sample units as stands, stand segments, and plots, any area which is large enough to escape the influence of direct interspecific biotic reactions.

The frequency distribution patterns of the Trempealeau species in Table III are reflective of normal, Gaussian distributions, although some of them have an occasional irregularity. The species peaking toward the left of Table III have a high presence in the upland forests of southern Wisconsin (Gilbert and Curtis 1953). The species peaking toward the right are found with high presence in Wisconsin prairies (Curtis and Greene 1949). Many of the species which peak in columns 2 through 4 are found on the presence lists of both the forest and prairie. Here is the vegetation of

TABLE IV. Indexes of interspecific association—Trempealeau*

	Osmunda	*Aralia*	*Eupatorium*	*Geranium*	*Desmodium*	*Carex*	*Galium*	*Celastrus*	*Solidago*	*Amphicarpa*	*Euphorbia*	*Monarda*	*Amorpha*	*Andropogon*	*Coreopsis*	*Rosa*
Osmunda c.		14	—	09	16	—	—	—	13	—	—	—	—	—	—	—
Aralia n.	*35*		01	*49*	*47*	03	*31*	*17*	*04*	08	09	—	—	—	—	-
Eupatorium r.	82	*51*		*12*	*26*	*09*	*07*	10	*18*	19	09	—	—	—	—	—
Geranium m.	15	*28*	*21*		*19*	*05*	*07*	*05*	*30*	*14*	—	07	—	24	09	*09*
Desmodium g.	27	*28*	*21*	*30*		*03*	*11*	*21*	02	08	30	40	—	*72*	44	17
Carex p.	79	*17*	*42*	*18*	*10*		06	13	*06*	*09*	00	07	66	*55*	09	21
Galium b.	89	09	*24*	*08*	*11*	*08*		07	*02*	09	06	33	15	23	*36*	17
Celastrus s.	82	*05*	*14*	20	01	00	*09*		*12*	05	24	06	12	29	07	24
Solidago u.	56	38	22	*28*	*00*	08	*14*	*18*		*18*	*02*	*23*	*10*	*29*	*06*	*07*
Amphicarpa b.	82	23	08	*25*	*01*	36	*16*	*10*	*30*		02	00	08	08	*15*	13
Euphorbia c.	100	62	39	42	59	*05*	*04*	28	*12*	*20*		*02*	00	03	*32*	05
Monarda f.	100	80	62	23	40	26	14	*02*	*27*	*29*	*12*		*10*	14	00	00
Amorpha c.	100	44	10	27	63	*14*	*04*	*02*	*22*	*18*	*19*	*05*		*37*	*30*	05
Andropogon g.	100	88	53	45	76	*05*	01	20	*16*	*11*	*17*	*05*	*51*		*21*	*13*
Coreopsis p.	100	92	71	41	70	74	*26*	09	*33*	*29*	*32*	*26*	*35*	*37*		*06*
Rosa a.	100	100	100	43	57	63	23	33	*19*	01	*17*	*35*	*23*	*39*	*43*	

*The left-lower half of the table shows Cole's Interspecific Association Values for 16 common species among all the Trempealeau quadrats. Those values which are italicized are positive values and those not italicized are negative values. The values with bold-face type give a significant or highly significant association when tested with Chi-square. The right-upper half of the table shows Cole's indexes figured for only the quadrats of those plots which contain both species. The cells with single dashes represent association based upon probabilities too small to be tested with Chi-square.

two formations coming together within the oak opening transition of the prairie-forest border and interlocking so smoothly that of those species which reach their greatest frequency within the oak opening, roughly columns 3 and 4, it is difficult to state whether they are primarily forest plants or prairie plants.

On the other hand, on the level of interspecific association where an index recognizing an expected random occurrence is utilized, it is incorrect, as was demonstrated, to measure interspecific associations within areas large enough to contain a varying community structure composed of a series of species with overlapping amplitude curves.

The relationship between amplitude behavior and degree of interspecific association should be, if these two features are genuine measurements of different levels of mutual occurrence, an independent one. The average index of amplitudinal correspondence of the 10 Trempealeau species combinations which are significantly positively associated is 65.0. The average index of the 7 significant negatively associated combinations is 62.1, while the average index for the species as a whole is 62.6. In both cases, there is a non-significant deviation of the index of amplitudinal correspondence from chance expectation and, therefore, a lack of correlation between amplitude and interspecific association information.

Although no detailed study with a graduated set of quadrats was made to determine the exact nature of the factors influencing association, the

TABLE V. Indexes of interspecific association—Butte de le Chien*

	Andropogon s.	*Helianthus l.*	*Amorpha c.*	*Stipa s.*	*Andropogon g.*	*Corylus a.*	*Galium b.*	*Rosa a.*	*Amphicarpa l.*	*Helianthus s.*
Andropogon scoparius		*18*	*50*	*61*	25	21	00	00	—	—
Helianthus laetiflorus	62		*58*	*09*	*25*	*34*	05	*21*	—	—
Amorpha canescens	*91*	92		*77*	62	*69*	09	00	00	00
Stipa spartea	*76*	*60*	*63*		*06*	16	19	06	21	*13*
Andropogon gerardi	16	*31*	*74*	*14*		*53*	16	06	14	12
Corylus americana	40	12	05	12	*23*		03	03	18	03
Galium boreale	26	36	04	23	14	*10*		*33*	*37*	*44*
Rosa arkansana	20	20	06	05	03	06	*42*		*23*	*100*
Amphicarpa bracteata	100	100	46	59	30	*05*	*25*	*32*		*28*
Helianthus strumosus	94	90	44	69	20	*30*	*19*	*20*	*89*	

*The left-lower half of the table shows the Cole's Interspecific Association Values for 10 common species among all the quadrats of Butte de le Chien. Those values which are italicized are positive values and those not italicized are negative values. The values with bold-face type give a significant or highly significant association when tested with Chi-square. The right-upper half of the table shows Cole's indexes figured for only the quadrats of those plots which contain both species. The cells with single dashes represent association based upon probabilities too small to be tested with Chi-square.

light intensity readings did give some information in a few cases. If a microgradient exists within the 10 x 10 m. plots, then some of the 7 pairs of species which are negatively associated should show a marked difference of average light intensity on those quadrats in which the species are not found together. This marked difference can be expressed as a ratio between the species with the higher average light intensity per quadrat and the species with the lower average light intensity. The two negatively dependent species combinations showing light intensities per quadrat of a striking difference were *Desmodium* with *Monarda* and *Desmodium* with *Andropogon.* In those plots in which they both occurred, the average light on the quadrats containing *Desmodium* was 1,085 foot candles and on those quadrats containing *Monarda* was 4,437. The ratio of the average intensity of *Monarda* to *Desmodium* was 4.08. In those plots containing both *Desmodium* and *Andropogon,* the average intensity on the quadrats with *Desmodium* was 1,211 foot candles and on those containing *Andropogon* was 3,741 foot candles for a ratio of 3.00. The above two illustrations can be said to show a negative dependence due to a differential preference of the species for those differences in light intensities which exist in oak opening plots. The other negatively dependent species show an average light ratio of 1.37 which can be compared with an average ratio of 1.56 for the 10 species combinations which were most nearly independent. This suggests that their dependence is determined by factors other than light preference.

Descriptions of species mutuality

If the mutual occurrence of *Desmodium glutinosum* and *Andropogon gerardi* were being described for the Trempealeau prairie-forest border, it could be said that they have amplitude curves which peak in different parts of the constructed ordination, *Desmodium* growing best toward the forest and *Andropogon* toward the prairie. Their amplitude curves show a moderate amount of overlap and within this overlap area they have a negative association which is highly significant. *Galium boreale* and *Coreopsis palmata* also show a moderate degree of overlap, *Galium* peaking in the middle of the ordination and *Coreopsis* toward the prairie end. They have, however, a significant positive association within the overlap area. *Coreopsis palmata* and *Rosa arkansana* have amplitudes which peak in the same part of the ordination with a high amount of overlap, and both are found toward the prairie end. Within the overlap area they are independently associated. The relationships of the other species can be described in a similar fashion.

SUMMARY

The mutual occurrence of species as they appear within common geographic areas may be described by: (1) the degree to which the species share similar ecologic amplitudes and can be found in the same stands or plots and in the same part of a phytosociologic ordination; and (2) the amount by which they are associated in the quadrats of those stands in which they mutually occur.

To determine the degree to which species share similar amplitudes, the plots of a transect study of an oak opening were arranged into a linear order based on a plot index whose values depended on the adaptation values assigned to the 16 most frequent species. These adaptation values were determined from a matrix of indexes of amplitudinal correspondence which represented the joint occurrence of the species together by plots as a percentage of their average individual plot occurrence.

As an independent check, a second ordination of the oak opening plots was undertaken in which the position of each plot within a linear order was determined by the amount of its quantitative vegetational similarity to the other plots. The measurement of similarity was based upon the computation of a matrix of Gleason's modification of Jaccard's Coefficient of Community.

The two ordinations were shown to have a highly significant rank correlation.

The mutual occurrence of species on a community level was demonstrated by frequency distributions which showed amplitude curves which were variable in size, had shapes which resembled normal distributions, and formed continuous and smoothly interchanging spatial patterns.

The mutual occurrence of species on the level of interspecific association was computed with Cole's index, using for each index value only the quadrats of those plots which contained both species in order to eliminate the influence of varying ecologic amplitudes on interspecific association. The great majority of species in two oak opening transitions were shown to be independently associated. The association of those species which showed a significant dependence was not determined, for the study in which plot ordinations were constructed, by the relative distance of the species from each other along the ordination. The influence of light microgradients within plots was found to be correlated with two of the 17 associated species combinations.

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MICROCLIMATE AND A RELIC STAND OF *TSUGA CANADENSIS* IN THE LOWER PIEDMONT OF NORTH CAROLINA

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INTRODUCTION

Tsuga canadensis, a typical component of the northern hardwood forest, ranges from the Lake States to New England and then down the Appalachians as a member of the mixed mesophytic forest. Along the southern fringes of its range, it often occurs in widely isolated outlying situations which are completely surrounded by ecologically unrelated vegetation. These disjunct hemlock communities have attracted attention and study sufficient to permit certain generalizations as to their probable history and the conditions which allow their continued survival.

Numerous disjunct occurrences of *Tsuga canadensis* in Alabama were reported by Harper (1928, 1937) as commonly appearing in ravines with other Appalachian species in association. An excess of evaporation over precipitation was suggested as limiting the range of the species southward and it was pointed out that most stations were in close proximity to a permanent stream with attendant local humidity probably higher than that of the surrounding area (Harper 1952). Another report on these Alabama hemlock communities (Segars, *et al.* 1951) includes a map of their distribution and refers to them as relics of a more wide-spread Pleistocene distribution. On the basis of atometer measurements made in June and July, persistence of these hemlock relics is attributed, in part at least, to the relatively high humidity of the habitats.

Disjunct hemlock stands in Indiana have been studied intensively (Daubenmire 1931, Friesner and Potzger 1931, 1934, 1936, 1944, Potzger and Friesner 1937). The community is considered as a segregate of a Tertiary climatic climax, more widespread in the Pleistocene and post-glacial period but progressively restricted until now it survives only in special habitats as a relic with numerous other species of northern distribution in association. The *Tsuga* is restricted to isolated steep slopes and canyons where, by actual measurement, the evaporation rate is higher, soil moisture is lower, and soil pH and depth are less, than on the sites which support the *Fagus-Acer* climax. Thus, microclimate permits survival of *Tsuga* because the more mesophytic species of the climax are excluded. Very similar conclusions were reached after comparing hemlock and *Fagus-Acer* sites in New England (Moore, *et al.* 1924).

It is important to note that Friesner and Potzger also recognize a *Quercus-Carya* association in Indiana and that they consider the *Tsuga* sites to be more mesic than those occupied by *Quercus-Carya*.

In North Carolina, an association of characteristically mountain species occupies an area no greater than 3 or 4 acres on a river bluff in the lower Piedmont. The most conspicuous examples are *Tsuga canadensis*[1] and *Quercus prinus* in the overstory, and *Hydrangea arborescens* and *Galax aphylla* in the shrub and herb layers, respectively. The vegetation surrounding the area is typical of the lower Piedmont with some fields in cultivation, others in various stages of succession after abandonment, and some areas of oak-hickory forest (Oosting 1942).

Because the community of the bluff is disjunct from its normal range by some 200 mi. and is here so sharply restricted, a study of its make-up and the factors of the local environment was outlined with the objective of learning, if possible, something of the special circumstances permitting its survival here. Because the hemlock appeared to be the species most widely removed from its normal range, the study was centered on it and particularly on the microenvironment affecting the hemlock seedlings.

Financial aid from the Research Council of Duke University made the study possible.

THE STUDY AREA

The site is a north-facing bluff overlooking Swift Creek in Wake County, North Carolina, about 10 mi. west of Raleigh. It is ¼ mi. north of the present intersection of roads running east (4.5 mi.) from Apex and south (5 mi.) from Cary. The region is rolling and well-drained. Soils of the uplands are residual and derived from various types of parent rock. Elevations range from 90 to 150 m. above sea level.

Although there are today only 11 mature trees of *Tsuga canadensis* here, the bluff is known in the vicinity as "Hemlock Hill." In 1883, Holmes described the area briefly and mentioned that, in addition to several smaller individuals, there were 5 trees which measured 30-38 cm. in diameter near the base and about 15 m. tall. Coker and Totten (1934) referred to visits to the site in 1916 and 1933. On the second visit, 11 mature trees were counted (the largest, 56 cm. in diam.) and a few saplings and seedlings, fewer than in 1916. Still another brief mention, without quantitative details, is made by Oosting (1942).

The bluff is the truncated northern end of a north-south ridge whose bevelled upper portion drops about 7 m. to the bluff face that rises about 23 m. from the floodplain as a vertical rock face or at less steep angles of 35° to 40°. The base of the portion facing north extends for 150 m. from its eastern edge to a point where it curves to the northwest and the bluff rapidly decreases in height. At one point, the face is deeply incised by a bifurcated cove. There is active undercutting by the small but permanent stream which flows east and south around the base. Across the stream is a wooded flood plain that extends northwest, north and east, with gentle rises to other ridges at distances of half a mile or more (Fig. 1).

Soil

The soil of the main body of the ridge is of the Cecil series with an A horizon of gray sandy clay or sandy clay loam, 5-10 cm. deep, over a B horizon of red to reddish-yellow, plastic clay which extends to at least 40 cm. Several veins of quartz outcrop on the ridge and quartz fragments of all sizes are abundant in and on the surface of the soil.

The soil of the bluff, especially the steeper portions, is a yellow loam with no profile development and uniform texture down to the parent material, a very fine, micaceous schist, which lies at a depth of 25-40 cm. The soil mass is loose and porous. Along much of the lower half of the bluff the parent material is exposed in the partially weath-

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[1] Nomenclature follows Fernald (1950).

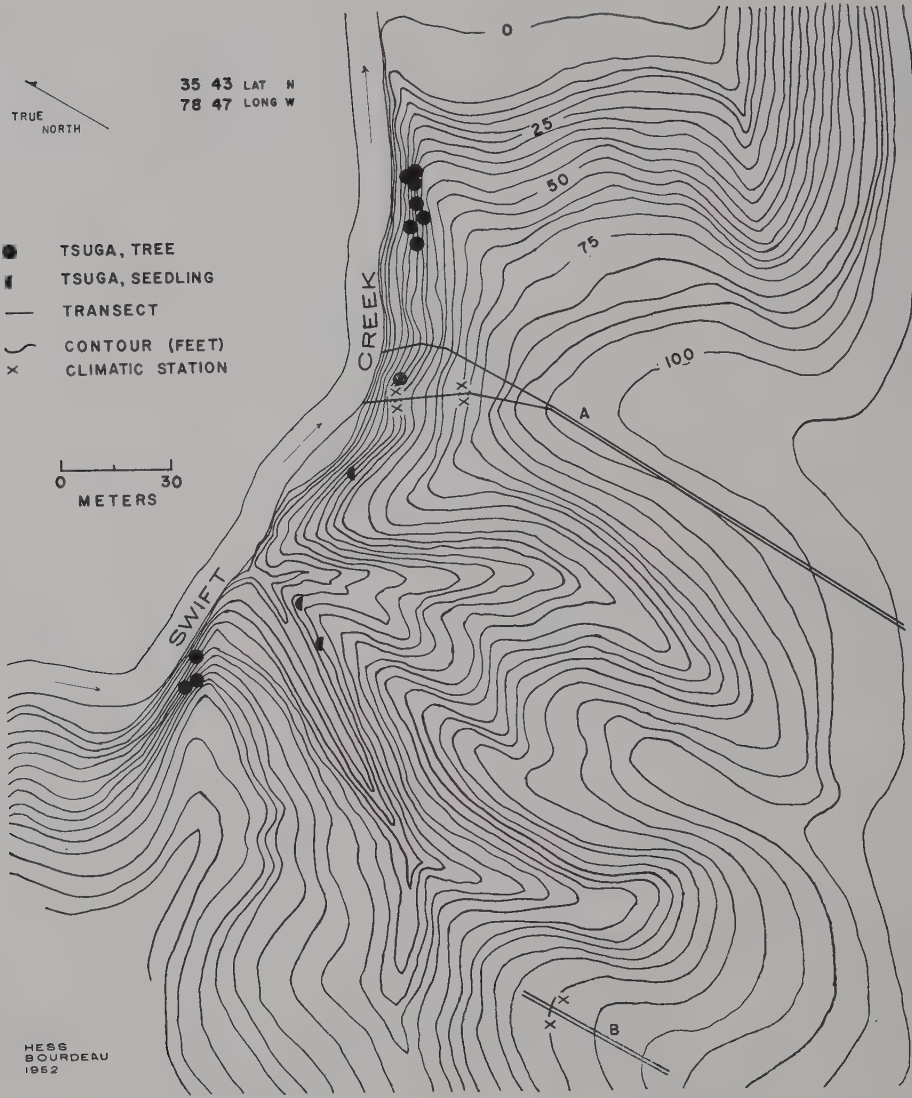

Fig. 1. Contour map of the study area. The pair of X's to the left on transects A, represent climatic Station I, those to the right, climatic Station II, and the pair on transects B, climatic Station III. The three half circles represent three seedlings which are isolated from a seed source. The numerous seedlings found in the immediate vicinity of mature *Tsuga* are not shown on the map.

ered rock faces and boulders. The pH of soils of the bluff and the ridge ranges between 5.0 and 5.5.

Vegetation

The region surrounding the bluff, and on the ridge itself, where flat enough, is a patchwork of cultivated, or abandoned fields in various stages of secondary succession. The floodplain opposite the bluff supports young pine stands, 15-30 years of age. Along the bank of the stream are typical bottomland hardwoods such as *Platanus occidentalis, Liriodendron tulipifera, Betula nigra,* and *Carpinus caroliniana.*

On the ridge and adjoining the study area to the southeast, is a cultivated field some 5 acres in extent. To the south and southwest is an even-aged 40-year pine stand, indicating cultivation in the past. These areas are 180 m. back of the bluff. West of the bluff is pine forest which has been selectively cut.

A comprehensive survey of the flora of the bluff was made but the majority of the species appear to have no particular bearing on the present problem. Significant species are presumed to be included in the transect data.

Distribution of vegetation on the bluff was determined by means of transects extending 170 m. from the creek, up the bluff face, over the bevel, and up the ridge to the bounding vegetation types just described. Two strips (A on the map, Fig. 1) 2 m. wide were used beginning 15 m. apart on the bluff face and running side by side on the bevel and ridge top. On a meter's width of each strip all vegetation was tabulated while in the full 2 m. strip, trees (individuals over 5 cm. d.b.h.) were tallied. Later, an additional short transect (B on map) was run at climatic station III which had not been established initially.

Four major sections of the bluff, each arbitrarily 44 m. long, were recognized for interpreting transect data: (1) bluff face (a. lower, b. upper, each 22 m.); (2) bevel; (3) forward portion of bluff top; (4) rearward portion of bluff top bordering other plant communities.

To show the changing composition of lesser vegetation in the several segments of the bluff, the number of individuals of a species which occurred in each segment of the transect was expressed as a percentage of the total individuals of that species found in the entire transect. The change in abundance from one portion of the bluff to another is shown for the 8 most numerous herbs (Table I).

TABLE I. Relative abundance of the most numerous herbs on the several segments of the bluff. The number of individuals in a segment is expressed as a percentage of the total individuals of the species in the transect

Species	Face a	Face b	Bevel	Forward	Rear
Athyrium asplenioides	100				
Polystichum acrostichoides	100				
Luzula echinata	100				
Galax aphylla	40	60			
Smilax rotundifolia	4	9	43	0	44
Panicum spp.	2	6	66	26	0
Compositae (spp.)	0	1	13	81	5
Chimaphila maculata	0	0	40	42	18

It is immediately apparent that these principal species occur in zones with the ferns and *Luzula* strictly limited to the lower bluff face, *Galax* extending higher but not into the bevel, and *Chimaphila* (an upland species) restricted to the upper zones. Not shown in this table is a further restriction in the fern distribution. Of the *Athyrium,* 94% occurred in the first 11 m., 6% in the second 11 m. from the creek. *Polystichum,* however, was 83% in the second 11 m. and only 17% in the first. *Luzula* was 90% in the first 11 m. and both *Galax* and *Smilax* were almost excluded from this lowest sub-zone. Where there is a narrow bit of floodplain at the base of the bluff, it invariably supports *Xanthorhiza simplicissima.*

Three kinds of shrubs and four of tree seedlings show a distribution somewhat correlated with the topography (Table II). Species typical of the surrounding upland forest were concentrated in the upper part of the area while more than half the seedlings of *Quercus prinus* were in the segment just above the bevel.

TABLE II. Percentage of three shrubs and four kinds of tree seedlings, in each major section of bluff transect

Species	Face a	Face b	Bevel	Forward	Rear
Gaylussacia frondosa	6	80	0	0	14
Vaccinium tenellum	0	0	80	20	0
Vaccinium vacillans	6	10	41	31	12
Styrax grandifolia	4	6	40	6	44
Acer rubrum	3	7	35	43	12
Quercus prinus	6	8	13	51	22
Quercus spp.	0	0	25	19	56
Carya spp.	0	0	6	33	61

The relative importance of the major overstory and understory trees is indicated by topographic divisions in Table III. Basal area (dm.^{2}) and the number of understory individuals (less than 5 cm. d.b.h, more than 3 m. tall) is given for each species by transect segments. The superior development of upland oaks and pine in the rear segment is notable, but to be expected. The general distribution of *Quercus prinus,* with a concentration high on the bluff face and bevel, was also predictable from observation.

TABLE III. Basal area (dm^2) and the number of understory individuals (in parenthesis) of seven tree species on segments of the bluff

Species	Face	Bevel	Forward	Rear
Oxydendrum arboreum	2.68(4)	.63(5)	.32(16)	2.41
Acer rubrum	3.84(2)	.97(6)	2.55(11)	.78(1)
Styrax grandifolia	.51(4)	.08(5)	.50(2)	4.56
Cornus florida	......	(1)	......	2.37
Pinus spp.	......	13.52	20.37	107.67
Quercus prinus	30.80	2.65(2)	16.09(1)	1.32
Quercus spp.	......	32.28	......	249.16(1)

Fagus grandifolia did not appear in the transects but it contributes partially to the overstory of the bluff. Several individuals grow along the base of the slope, 1.5-2.5 m. above the level of the narrow floodplain (Fig. 2).

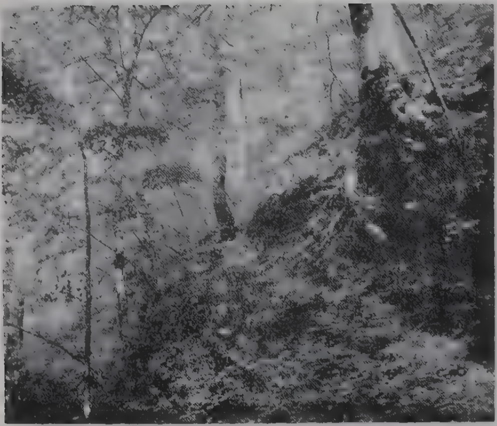

FIG. 2. A lower portion of the bluff showing *Fagus grandifolia* about 2 m. above the stream. The tree in the center is the "central" *Tsuga* (d.b.h. 46 cm.).

Finally, the numbers and distribution of hemlock trees and seedlings must be detailed. There are 11 individuals of tree size and all occur on the bluff face at 9-12 m. above the stream level. The distribution is in three groups with 7 trees at the eastern extremity of the bluff, one isolated near the central portion, and 3 near the western end (Fig. 1). All occur along the upper edge of exposed vertical rock faces.

The trees are not even-aged. They range from 20 cm. to 56 cm. d.b.h. and from 10 m. to 22 m. in height (Table IV). The smaller trees are all overtopped and they present a very poor appearance. The larger trees seem thrifty, except for one which has the top broken out about 9 m. above the ground and retains only one fairly large growing branch. This tree, 43 cm. d.b.h., and one other (38 cm. d.b.h.) were used for increment borings as were two smaller ones (25 cm. and 20 cm. d.b.h.). The larger trees are between 300 and 350 years of age and the smaller ones, 50-75 years. The size and location of each tree is given in Table III.

TABLE IV. Diameter and height of the 11 mature *Tsuga*. "Broken" means the top has been broken out at the indicated height above the ground. "30°" refers to an individual growing out over bluff face at this angle from the horizontal

Trees	d.b.h. (cm)	height (m)
East Group	20	11
	23	11
	20	11
	38	21
	48	24
	43	23
	43	9 (broken)
Center Tree	46	23
West Group	25	9
	51	20
	56	24 (30°)

Hemlock seedlings occur in the vicinity of each of the three groups of trees but only along the lowest portion of the slope below the east and central group, and only on the upper part of the slope near the western group. On the map (Fig. 1) three isolated seedlings are indicated because they are the farthest removed from a seed source. The one on the open face of the bluff is in the .9-1.2 m. height class (Table V), the two in the cove, in the .3-.6 m. class. Six seedlings were found on the floodplain across the stream opposite the east group of trees. They ranged from 15-30 cm. tall.

TABLE V. Numbers of all *Tsuga* seedlings on the bluff by height classes (meters)

	0- .15	.15- .30	.3- .6	.6- .9	.9- 1.2	1.2- 1.5	1.5- 1.8	1.8- 2.1
East......	31	17	11	2	1	0	0	1
Center....	30	10	4	1	0	0	0	0
West......	84	35	22	5	0	0	0	0

MICROCLIMATE

Methods

A year's study of the climate of the bluff was planned in the hope that the data would be indicative of the factors permitting survival of the species disjunct in their ranges. Procedures were specifically related to *Tsuga* seedlings since conditions affecting their establishment and survival might well be the most critical ones.

Initially, the plan was to compare the physical factors of the bluff with those of some near-by upland site supporting oak-hickory forest (climax). But, no such satisfactory stand is located within reasonable distance of the bluff and the plan was altered to compare the conditions of the bluff face supporting *Tsuga* seedlings, with those on the bluff top, behind the bevel, in mixed hardwood-pine, where no *Tsuga* seedlings occur although it is well within dispersal range of the seeds. Accordingly, in August, 1952, stations were established at two levels: Station I, on the bluff face on the 10 m. contour; Station II, on top of the bluff 15 m. back of the bluff face. Later, November, 1952, Station III was initiated in the south-west portion of the study area at the head of the cove which cuts into the bluff here. At each station, paired observations were made at points 10 m. apart on the contour. Measurements as given are therefore averages of replicated observations.

Observations were made for 3 consecutive days once every month, except that two such sets of data were obtained in the initial months, August and September, 1952, and that February, 1953 was omitted. The last observations were for July, 1953. Measurements were recorded at 2-hour intervals beginning just after sunrise and ending at sunset. Nightly observations were not made systematically. Thus, all summaries and plotted data points represent averaged two-hourly observations made during daylight hours of three consecutive days. Numerous visits at shorter intervals were made to obtain moisture and temperature data from instruments permanently installed in soil and litter.

Temperature.—Measurements at each station were made at four levels: 38 cm. and 5 cm. below the soil surface, on the surface between litter and mineral soil, and 15 cm. above the soil. All instruments were standardized against each other.

At each station one recording hygrothermograph was used at the 15 cm. level but all other measurements in this series were made with mercury-in-glass thermometers. In the soil, these were lowered in holes bored to the desired depth and of a diameter slightly larger than the thermometer. Each soil thermometer had a very small glass tube filled with 70% alcohol closely fitted over the bulb to act as a damper and allow raising the thermometer (with tube) for reading without appreciable temperature change.

For surface temperatures, the thermometer was inserted and left under the litter and read without exposing the bulb. Air temperatures at the east position of each paired observation were obtained with Friez hygrothermographs set on small wooden frames to raise the temperature element 15 cm. above the ground. A sheet of aluminum foil was placed loosely over each instrument as a shield against insolation but still permitting ventilation. To keep the sensitive elements facing away from the sun the instruments were turned at regular intervals. The other air temperature measurement of each pair was made with a mercury-in-glass thermometer mounted in a wire holder backed with a concave aluminum shield to protect against insolation. These too were turned to expose the thermometer away from the sun.

To obtain an indication of temperatures between regular visits, a grid pattern of Taylor maximum-minimum registering thermometers ("Six's") was placed on mineral soil under 2-3 cm. of litter. Nine were placed on the bluff face with 3 along the 2 m. contour, 3 at the 10 m. contour, and 3 at the 30 m. contour. A pair of these was also placed at both Stations II and III.

Humidity.—In addition to the hygrothermograph record for each station, humidity was determined at 2-hour intervals with a cog type, wet-dry bulb psychrometer whirled within 5 cm. of the ground.

Evaporation.—Two sets of Livingston atmometers in pairs, one white and one black, and equipped with mercury rain traps, were operated at each station during the 3-day periods. The center of each bulb was 25 cm. above the ground.

Light.—By the use of two photoelectric units it was possible to make measurements on the bluff face or bluff top and simultaneously to make observations in the open for comparisons with full sunlight. Measurements were made at local noon in October, while the trees were in full leaf but had changed color, and in December, just before the solstice, on days when the sky was clear or had no more than a slight haze. In the stands, 10 to 20 readings were made at 1 m. intervals along the contour of the stations, with the sensitive element of the instrument facing up, just over 1 m. above the ground, and unshaded by the operator. The instrument in the open was kept in a fixed position.

Soil moisture.—From August, 1952, until January, 1953, soil moisture determinations were made every 3-5 days, especially during dry intervals. Samples were taken with a soil auger from 5 cm. and 38 cm. depths, and the percentage soil moisture was calculated on the basis of oven-dry weight.

In January, 1953, two pairs of Colman fiberglass soil-moisture units were installed at 5 cm. and 38 cm. depths at each of the climatic stations. The units were forced into the side walls of small pits with their flat surfaces parallel to the soil surface. When the holes were refilled, the electrical leads were dropped several centimeters below the point of attachment before being returned to the surface to prevent seepage of surface water along the wire to the unit. After the period of field use, the fiberglas units were calibrated with the soils in which they were buried. Soil samples with the units in place, were brought to the laboratory and after soaking, electrometric measurements were checked against weights as the soil was gradually dried, to give a calibration curve.

RESULTS

Temperature.—Consistent temperature differences between the bluff face (Station I) and the bluff top (Station II) were measured throughout the year. Averages for each period of observation were plotted for each of the four levels measured at both stations (Fig. 3).

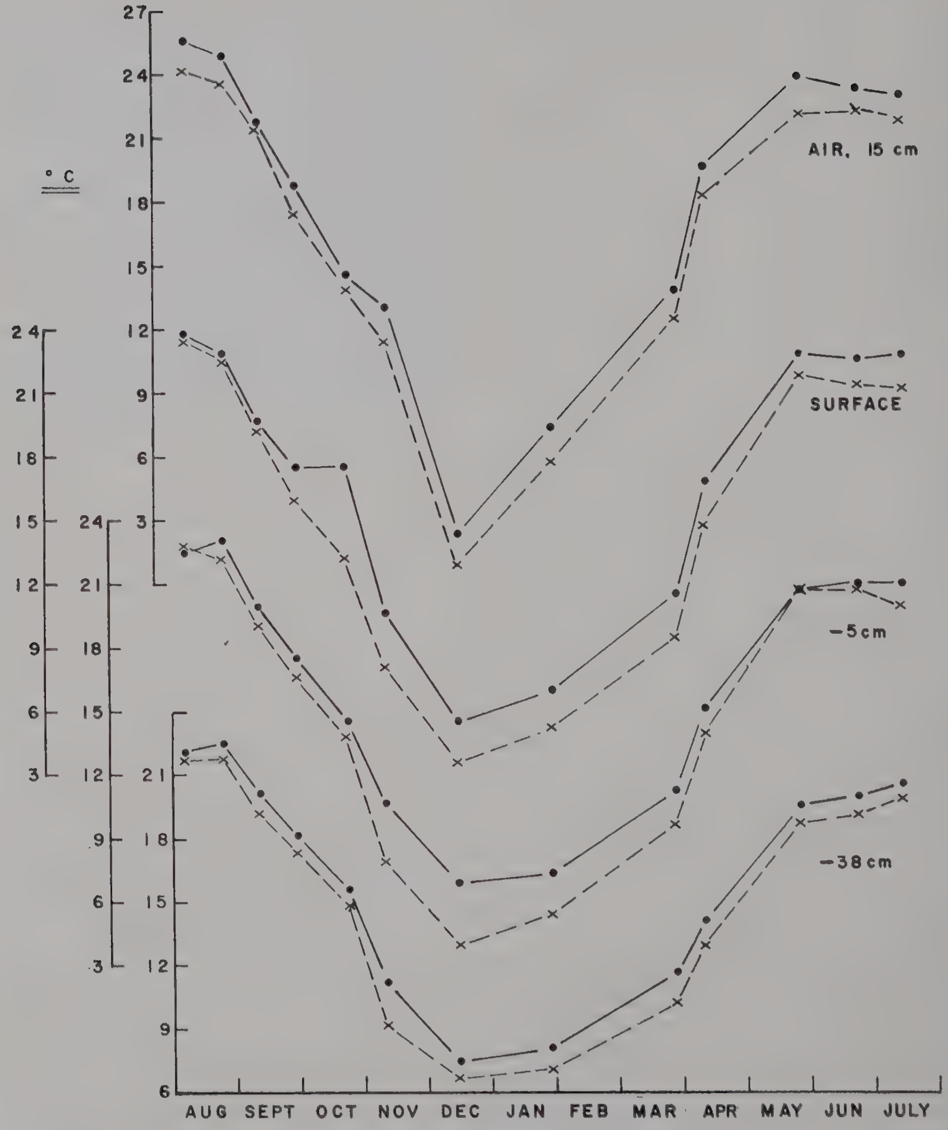

Fig. 3. Temperature trends throughout the year, at the four levels measured. The broken line represents the averaged data for Station I (bluff face) and the solid line is for Station II (bluff top).

At all levels, the temperatures on the bluff face were lower than on the bluff top. At the 38 cm. depth this difference averaged 1.1° C for the year, with the greatest mean difference occurring during the winter after leaf-fall, 2.2° C in December, and the least during the summer months, 0.6° C in August, and 0.7° C in July. At the 5 cm. depth, the average differences were again 1.1° C with the greatest mean difference in winter, December 3.0° C, and the least in spring, May 0.0° C. The only exception was in August (4-6) when the soil at 5 cm. on the bluff face averaged 0.1° C higher than on the bluff top. During this run, there were several heavy rains and general cloudiness, both of which may obscure microclimatic differences (Geiger 1950).

Temperatures at the soil surface followed the same trend, with the upper station having a mean

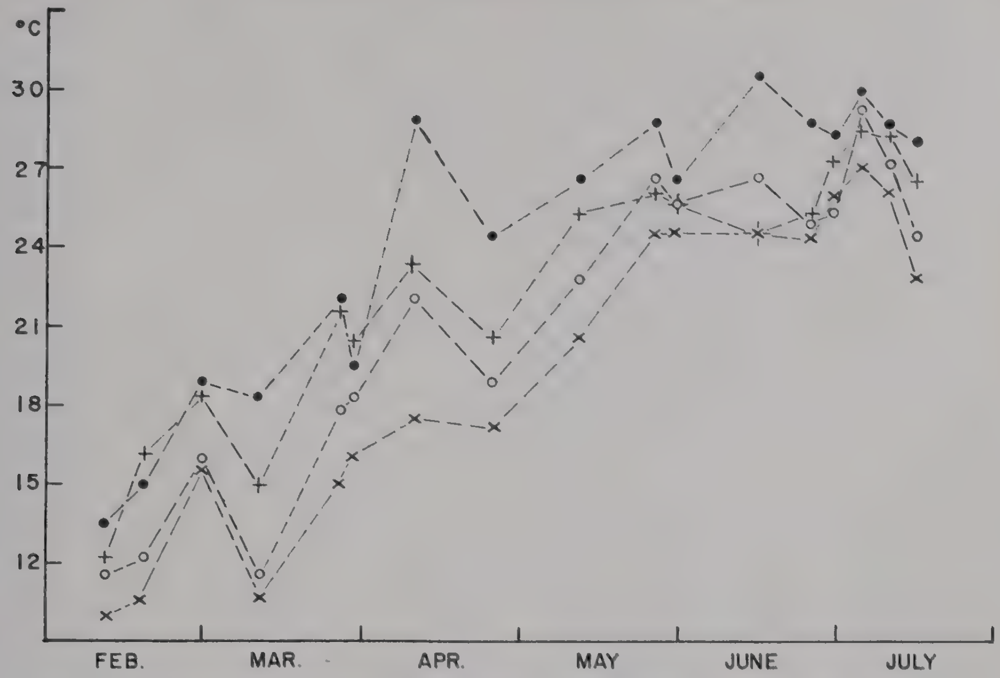

Fig. 4. Maximum litter temperatures at four contour intervals above the foot of the bluff: × = 2 m. above, O = 10 m., + = 30 m., and solid dots the top of the bluff (Station II).

average 1.7° C higher than the lower station. The least difference was in September, 0.3° C, and the greatest in October, 4.4° C, and December, 2.5° C. The air temperatures at 30 cm. were also higher on the bluff top but as might be expected, the average difference, 1.3° C, was slightly less than at the surface level and the mean differences for summer and winter did not vary as in the soil.

A positive correlation of increasing temperature with increase in height of the bluff was obtained from the measurements with max-min thermometers left in the litter. Maximum temperatures were lowest at the 2 m. contour on the bluff face, were successively higher at the 10 m. contour, and just below the crest of the bluff, and were highest on the top (Station II). These differences were most pronounced during winter and early spring. In summer, the relationship was not always linear (Fig. 4). The mean difference between maxima for the bottom and the top of the bluff was 4.8° C.

Minimum values obtained with the same instruments, also show clear correlation with position on the slope, especially during the late winter and early spring when they show an inverse relationship with increasing height on the bluff face. From February to April, the lowest temperatures occurred just below the upper edge of the bluff, at the 30 m. contour level (av. min. 0.4°), while the next lowest were on the bluff top (av. 1.8°), and successively higher minima occurred at the 10 m. (av. 2.0°) and 2 m. (av. 2.7°) contour levels. However, by late spring and early summer, all minima were so nearly the same, regardless of contour level, that they cannot be effectively shown graphically. Furthermore, variation at the four levels was inconsistent and apparently meaningless within the narrow range of differences (av. 0.9° C).

Humidity and evaporation.—Relative humidities for day conditions averaged 76% on the bluff face, and 70% on the bluff top. During the night, humidity was invariably much higher at all stations, commonly 100%. A more realistic comparison of conditions affecting evaporation and transpiration is possible when the vapor pressure deficit (V.P.D.) is known. For the lower station on the bluff face, the mean deficit was 3.8 mm. Hg, while the average of maximum deficits was 5.4 mm. At the upper or bluff top station the average mean value was 8.1 mm. Hg and the average maximum was 12.5 mm. Hg. For every monthly series of observations, the average V.P.D. of the upper station exceeded that of the lower. This was also true of the maximum V.P.D., except in September. The average difference was greatest in June (3.4) and July (2.5), and the least in

December (0.7), January and March. Obviously, atmospheric conditions, near the ground and most affecting seedlings, were such that a higher potential evaporation, and therefore also transpiration, would be anticipated on the bluff top than on the face.

Evaporation losses from Livingston atmometers, operated with bulbs at seedling height, were in accordance with the vapor pressure differences. The average of losses from the white bulbs on the bluff top (34 cc./48 hr) was 78.9% greater than for those on the bluff face (19 cc./48 hr). Losses from black bulbs in the same situations (av. 41 and 24 cc./48 hr) were 70.8% higher at the bluff top than the bluff face station. Depending upon atmospheric conditions, the differential between face and top was sometimes 100% or even more, for both white and black bulbs, and this was true both during periods of low and high evaporation.

Light.—Black and white atmometer bulbs were used in replicated pairs in the hope of obtaining an expression of the differences in solar radiation at the two stations. The average difference in absolute evaporation losses from black and white bulbs was slightly greater on the bluff top than on the face (7 cc. versus 5 cc./3 day period), as might be expected. But, the losses from black bulbs exceeded that from white by 26.3% on the face while the difference on the top was only 20.6%. It is apparent that the differences in solar radiation at the two stations are not fully reflected in the evaporation rates. The radiation effect must be differentially counteracted by other factors such as the consistently higher night temperatures and the higher humidity on the bluff face.

The limitations of a photoelectric meter for evaluating light in the forest are well-known. Only the general values need therefore, be given. With the trees in full leaf, the average of measurements on the bluff face indicated a reduction of full sunlight there to only 7.4%, while the bluff top received 9.8%. At about the December solstice, the measurements showed 12.4% on the face and 22.2% on the bluff top.

These figures are at least suggestive of the relative amount of canopy at the two stations and its effectiveness in reducing light in summer. Also, the increased difference between stations in winter, without much canopy, is as might be expected because of the position of the sun. Inadequate as these values may be for evaluating light, they are contributing evidence in support of the difference in temperature at the two stations and related effects on the moisture regimes.

Soil moisture.—Soil moisture at the two stations and at the two depths (5 cm., 38 cm.) showed consistent seasonal trends with minor fluctuations related to individual periods of precipitation.

Since the permanent wilting percentages at the 5 cm. and 38 cm. depths are 13% and 10% for the bluff face soils and 9% and 20% for the bluff top, all values are expressed in terms of available water to permit direct comparison. On this basis, at both stations, there was always more water available at 38 cm. than at 5 cm., except occasionally after a light rain which wetted only the surface soil.

Determinations of soil moisture were concentrated in the growing season and particularly during dry spells, on the assumption that differences at such times would be most meaningful. Only a few were obtained in winter when the soil was usually near field capacity and sometimes frozen. The averages of all determinations are therefore assumed to be representative of real differences. In these calculations, one extremely high value (I-38 cm.-32%) and one low value (II-38 cm.-1%) have been left out because they appear to be in error for no understandable reason.

Available water at 5 cm. averaged 15% on the bluff face and 11.2% on the top, while at 38 cm. the averages were 18.8% and 14.5% respectively. Thus, the bluff face, on the average, had a distinct advantage in available soil moisture at both depths.

The same generalization applies to seasonal differences, with but one exception. If the few determinations made in winter and very early spring are representative of the periods when soil moisture is plentiful in all circumstances, it appears that available water at 38 cm. on the bluff face is then somewhat lower than on top of the bluff. The most pronounced differences between the bluff face and the top occurred in the fall while the trees were still in full leaf and temperatures remained relatively high. After a relatively dry August, precipitation in the next 3 months continued below normal and available water became progressively lower and lower. But, the reduction was much more marked on the bluff top (to 3% at both 5 and 38 cm.) than on the bluff face (to 13% at 5 cm.; 15% at 38 cm). The average difference between top and face for fall was 8.5% at 5 cm. and 10.7% at 38 cm. Considering that the bluff top soil was near the wilting percentage during much of this period, it is apparent that these months could have been critical for survival on the bluff top of seedlings which might be under no stress on the bluff face.

Discussion and Conclusions

That the vegetation of this north-facing bluff is unique for the lower Piedmont of North Carolina is apparent on cursory examination. By means of a transect study it was established that the distinctive species have a distribution on the bluff closely aligned with its physiography. The trees of *Tsuga canadensis* are all restricted to the bluff face in a zone 9-12 m. above the stream. *Quercus prinus* trees are largest and most abundant on the upper bluff face, but, unlike hemlock they also occur higher up on the bevel and there are even a few on the bluff top. Hemlock seedlings are restricted to the bluff face, with only one or two exceptions. Those on the lower face appear thriftier and darker in color than those higher up near the bevel and concentrated along the upper edges of exposed rock faces. There are none on the bevel or above it.

The line between bluff face and bevel is essentially the lower limit for all oak seedlings, except those of *Quercus prinus,* and the upper limit of *Galax aphylla.* This mountain species is abundant on the bluff face and up to the bevel where its occurrence terminates in an abrupt transition no more than a meter wide. Not so apparent, but again separated by the same line, is the concentration of *Gaylussacia frondosa* on the upper bluff face and its replacement by *Vaccinium tenellum* on the bevel. Thus, the distinctness and limits of the bluff face as a habitat are clearly indicated by several species, including three which are here disjunct in their ranges.

It was thus appropriate to concentrate the study of environment on the bluff face for comparison with the upland conditions on the ridge above. It was recognized that an adequate evaluation of the microclimate of a bluff is scarcely practical in terms of observations made at intervals during a single year. But, it was assumed that paired observations, with replications, in each of the two habitats could be fairly indicative of the environmental controls which determine the distinctive vegetation of the bluff.

Though there are differences in physical properties of the soil of the bluff and the ridge top, the boundary is not at all sharp, and the physical differences can hardly be correlated with the vegetation. In general, the soil on the bluff face is more porous and less compacted and the wilting percentage is lower than that on the bevel and ridge. Regardless of season or periods of drought, there was more available water in the bluff soils than in those of the bluff top and this could be a major determinant of the vegetational differences.

The microclimatic data for a zone extending from 38 cm. below the soil surface to 15 cm. above it, show temperatures consistently lower on the bluff face than on the ridge and that they increase constantly with ascent of the slope. Evaporation, vapor pressure deficit, and insolation are also less on the bluff face than on the ridge.

As has been indicated, measurements and procedures were planned in terms of hemlock and particularly of the conditions most affecting its seedlings. Other studies of hemlock, in Indiana and New York (previously discussed), have shown that it grows in areas with a less favorable moisture regime than that of the local beech-maple climax, and that the soils under hemlock were shallower, on the characteristically steep slopes, with a lower pH. In Alabama, disjunct hemlock stands are on rugged topography, near permanent streams where humidity is relatively high. The absolute range limit is assumed to approximate a line beyond which evaporation exceeds precipitation.

No observations of the North Carolina site are in disagreement with the generalizations about stands in Alabama. However, there are marked differences from the Indiana conditions. There, the soil moisture regime is less favorable than that of the climax (beech-maple), whereas in North Carolina the soil and atmospheric moisture are higher and temperatures are lower than in the upland forest. But, is this not as it should be? In Indiana, the bluffs are sufficiently drier than climax sites to exclude the mesophytic species of the climax while in North Carolina, the bluff is sufficiently cooler and moister than the uplands to give hemlock an advantage over oak-hickory on the site.

In Indiana, hemlock sites have moisture conditions intermediate between those of beech-maple and oak-hickory (Friesner and Potzger 1936). In North Carolina, beech grows along the base of the bluff, just above the floodplain, where moisture and humidity must be higher and evaporation less than on the face of the bluff. Again, *Quercus prinus* is concentrated near the top of the bluff and extends up on the bevel and bluff top where it gradually gives way to Piedmont oaks. In the mountains, hemlock is concentrated in coves, or locally, on occasional flats, which are cooler and moister than the surrounding slopes where *Quercus prinus* is commonly a dominant.

The association of these key species with major physiographic and climatic features in their general distribution is therefore, faithfully replicated on a small scale on this bluff. From the floodplain up the bluff to the ridge top there is a progressive increase in temperature, insolation, and evaporation, with a paralleling decrease in available water and atmospheric humidity. The sharpest breaks in this sequence appear to be at the upper edge of the floodplain, the top of the bluff face, and the top of the bevel. Each of these zones is marked successively by beech at the bottom, hemlock, with several lesser species, on the face, chestnut oak on the bevel, and Piedmont oaks and hickories on the ridge.

From fossil evidence (Buell 1945), it is known that Pleistocene vegetation of the Piedmont included species which now are components of the boreal forest. There must also have been species of more temperate requirements, such as hemlock and beech. The unavoidable conclusion, therefore, is that during the post-glacial period, as the southern range of these species became progressively constricted to the present typically montane limits, there was local survival of relic stands in specially favorable habitats. This hemlock stand appears to be such an outlying relic.

The microclimate contributing to the continued survival of the hemlock was the object of this study and the emphasis was placed on the seedling environment. Factors affecting the production of viable seed were not considered although it is certain that the microclimate of the *Tsuga* crown is quite unlike that affecting germination and survival of the seedlings.

Viable seeds are produced and some germinate since there are seedlings present. However, there are at present no individuals of sapling or pole-size. Several explanations for the absence of intermediate trees may be considered. There may be microclimatic or edaphic conditions which inhibit survival beyond a certain size but these conditions are not known. A more likely explanation, and one that is known to be operative, is the removal by man of seedlings of suitable size for ornamental plantings. This becomes the more reasonable when hemlock reproduction elsewhere is considered. It is generally agreed that hemlock has good seed years only periodically. Even then, germination is erratic (Baldwin 1934) and usually no more than 30-60% (Frothingham 1915). Mortality of seedlings is extremely high (88.3% in Indiana) and especially if a dry year follows the year of establishment. Even within the normal range of the species, reproduction is cyclic (Graham 1941) and greatest after disturbance or fire (Maissurow 1941). Absence of intermediate-sized individuals is apparently not uncommon in any hemlock area. If, as in the small North Carolina stand, those few attaining more than seedling size are subject to removal by man, it is not surprising that transgressives are rare.

It may be questioned if the microclimate of the measured years has been characteristic of the lifetime of the mature trees now present. Probably conditions have been changed many times during the past 100 years through the agency of man. Shifting cultivation on or near the bluff is indicated by even-aged pine stands of several ages, and timber and wood-lot cutting are indicated by decayed stumps on the bluff. These activities must have caused an increase of sunlight, a rise of temperature, and a drop in humidity. On the other hand, only a few hundred feet east of the bluff are the remains of an old dam and mill wheel, and indications of an old mill pond, whose proximity would have improved the moisture relations on the bluff face. The increment borings of hemlock show a period of greatly increased growth slightly over 50 years ago. Whether this resulted after release from suppression due to clearing or an increase in moisture related to the mill pond (Avery 1940), or a climatic cycle is not known.

This one-year study of the climatic conditions on the bluff has given some indication of the actual conditions under which *Tsuga* is reproducing. Insolation, temperature and moisture differences between the bluff and upland are slight but consistent; soil porosity and mechanical composition also differ somewhat. No one factor appears to be determinative and it is likely that the survival of *Tsuga* here is possible because of the interacting effect of slight differences in several factors.

How slight these differences may be is well illustrated by the environmental data (not presented) obtained at Station III (at the same contour as Station II) which differ even less from those of the bluff face where *Tsuga* is reproducing. Station III has the same soil features and vegetation as Station II but the canopy is less dense and the litter is deeper.

It is concluded that *Tsuga* is barely capable of reproducing and maintaining itself on the bluff and is surviving under conditions that approach the xeric extreme of its adaptability. Barring interference by man, the stand will probably remain for some time under present climatic conditions, but actually, the hemlock may be slowly dying out.

SUMMARY

1. A one-year study was made of the microclimate and edaphic conditions as related to the vegetation of a north-facing bluff in the lower Piedmont of North Carolina. Observations were concentrated on the zone of seedling growth, from 38 cm. below the soil surface to 15 cm. above it.

2. The situation is unique in that a stand of *Tsuga canadensis* with several other montane species in association occurs here, disjunct from the normal range by some 200 mi.

3. On the bluff face, where *Tsuga* occurs, insolation, temperatures and evaporation are lower and available soil moisture is greater than on the bluff top where hemlock is absent. There are also some differences in the physical characteristics of the soil but not in pH.

4. No single factor seems to be primary in the survival of *Tsuga* seedlings and the distribution of other species on the bluff. Rather, it appears that the slight differences in several factors must interact to produce the total effect.

5. Indicators of regional vegetation types occur on the bluff in a sequence of progressively more xeric zones from floodplain to bluff top. Beech is at the the base, hemlock on the bluff face, chestnut oak on the face and bevel, and typically climax Piedmont oaks are on the bluff top. The position of hemlock seems entirely appropriate.

6. This isolated community is interpreted as a relic of more widespread Pleistocene vegetation which almost entirely receded to the Appalachians during post-glacial time. The relic community has survived on the bluff because of the special microhabitat provided there.

7. Barring the interference of man, the *Tsuga* will probably remain here for some time under present climatic conditions. It is, however, in a marginal condition since reproduction is minimal. Actually, the hemlock may be slowly dying out.

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ENERGY FIXATION AND UTILIZATION BY NATURAL COMMUNITIES IN WESTERN LAKE ERIE

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From 1951 to 1955, the rates of energy fixation and utilization by natural aquatic communities in western Lake Erie were studied under near-natural conditions at all seasons of the year. The photosynthesis and respiration rates exhibited by communities concentrated by screening water through No. 25 silk bolting cloth, and by communities studied at their natural population density, are presented below. Measurements of respiration of bottom fauna are included. These are related to environmental variables and the energy flow is estimated for (1) the total community, (2) the fraction retained by bolting cloth, and (3) the bottom fauna.

METHODS

CO_2 absorption from water during photosynthesis, and addition during respiration, was measured by determining pH change with a Beckman meter. The relationship between pH change and CO_2 change was determined by differential titration of natural water with a 0.010 N NaOH solution. A sample titration is shown in Table I. Each milliliter of NaOH added will either change 10 µmoles of H_2CO_3 to $NaHCO_3$ (which is analogous to removal of 10 µmoles by photosynthesis) or will change 10 µmoles of bicarbonate to carbonate (which is analogous to removal of 10 µmoles HCO_3— from bicarbonate, thus converting to carbonate, during photosynthesis). The data obtained in such a titration are plotted on a graph which is used to convert pH changes observed during photosynthesis or respiration to corresponding CO_2 changes per liter of water. For example: a 0.79 g. minnow enclosed in a 125 ml. bottle for 20 min. caused a pH change from 8.47 to 8.28, representing a CO_2 change of 20 µmol./liter. The respiration rate is computed as

$$\frac{20 \times 0.125}{0.79 \times 0.33} = 9.6 \text{ µmol. } CO_2 \text{ evolved per g. (wet wt.) per hr.}$$

Although replicate titrations on a given water sample show close agreement, significant variations in the shape and slope of these curves are observed from day to day, and place to place. The method, therefore, requires that a graph be constructed for each different water sample used.

TABLE I. An example of differential titration using water from western Lake Erie

Ml. of 0.010 N. NaOH added to 1 liter	pH after each addition
0	8.02
1	8.10
2	8.20
3	8.31
4	8.42
5	8.49

Figure 1 shows a graph of CO_2 change against pH change for four different waters: (1) ocean water (Moberg, *et al.* 1934), (2) Sandusky Bay,[2] when total alkalinity was 80 ppm., as $CaCO_3$ (3) a sodium bicarbonate solution having a total alkalinity of 90, and (4) western Lake Erie water when total alkalinity was 90. This figure shows that the relationship between pH change and CO_2 change varies greatly from one water source to another. Moore (1939) has published equilibrium equations, which Dye (1944) used to construct nomographs, showing the relationship between pH, total alkalinity, and the three forms of CO_2. These equations indicate that for natural waters of identical total alkalinity the pH:CO_2 curves should be alike. If one applies the equations to the curve for the sodium bicarbonate solution (3) an excellent fit is obtained, but natural water from Lake Erie shows significant departures from the theoretical curve, and water from Sandusky Bay shows 2.5 times as much CO_2 change per unit of pH change as would be predicted by these equations. The discrepancy is not caused by $CaCO_3$ precipitation because it is evident in those portions of the curve where free CO_2 is abundant. Moore's equations, and Dye's nomographs, therefore, cannot be relied upon to provide the relationship between pH change and CO_2 change in natural water. Apparently, the presence of salts other than bicarbonate and carbonate exert an influence on the shape and slope of these curves.

The sensitivity of the pH meter as an indicator of CO_2 change depends on the slope of the

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[2] Unpublished data provided by Dr. A. G. McQuate, Heidelberg College, Tiffin, Ohio.

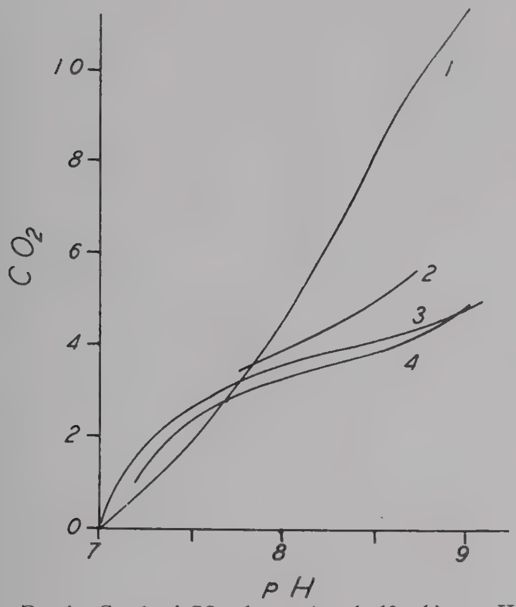

FIG. 1. Graph of CO_2 change (μmol./10 ml.) vs. pH change between values of 7 and 9. (1) represents ocean water, (2) Sandusky Bay water when total alkalinity was 80 ppm. as $CaCO_3$, (3) a sodium bicarbonate solution having a total alkalinity of 90, and (4) water from western Lake Erie with total alkalinity of 90.

pH:CO_2 curve. In western Lake Erie, the highest sensitivity is obtained between pH 8.0 to 8.5, which is also the range within which natural values usually lie. In this range, a pH change of 0.1 units represents a CO_2 change of about 12 μmoles per liter. The uncertainty of a determination with the Beckman meter is about 0.03 units, or about 3.6 μmol./liter. This sensitivity is similar to that of the Winkler method for O_2 determination (about 0.1 mg./liter, or 3.1 μmol./liter). In natural waters exhibiting a steeper slope in the pH:CO_2 curve, the sensitivity of the method is lower. In ocean water, the Beckman meter would indicate CO_2 change only one-fifth as sensitively as the Winkler method would indicate O_2 change. Sargent and Hindman (1943) overcame this obstacle by constructing a more sensitive pH meter. Many fresh water sources have a pH:CO_2 curve with a shallower slope than that of Lake Erie water, and in such waters the Beckman meter is more sensitive to CO_2 change than is the Winkler method to O_2 change.

In experiments using concentrated plankton, the communities were concentrated by passing water through No. 25 silk bolting cloth (0.064 mm. aperture) and resuspending in natural water to obtain suspensions of about 100 μliters of plant matter per liter. These samples were subdivided among a series of bottles, including a blackened bottle, and exposed to natural light at various depths for a period of 2 to 6 hours, near midday. Preliminary experiments in which exposure time was varied between 2 and 10 hours showed that the photosynthesis rates were fairly uniform during the first 4 to 6 hours, but declined markedly during the latter half of the period, approaching zero after about 8 hours in the light. Therefore, the test periods did not exceed 6 hours. The pH change during tests ranged from about 0.3 to 0.6 units. Thus, departure from natural pH levels was not large, and no significant precipitation of $CaCO_3$ occurred. After exposure to light, pH determinations were made, and the pH difference between the black bottle and each clear bottle was used to indicate CO_2 change at the respective light intensities of the clear bottles. The samples were then transferred to black bottles and returned to the lake for an additional 12 to 15 hour period to provide a measure of respiration rate. Samples were always tested as soon after collection as possible. When a sampling cruise required an entire day, the photosynthesis and respiration tests were made the following day. A subsample of the phytoplankton suspension was examined in a counting cell to determine phytoplankton volume per liter, and the photosynthesis and respiration rates were expressed as μmol. per 10 μl. of plant matter per hour ($1 \mu l. = 1 mm.^3 = 10^9 \mu^3$). The plankton from another subsample was transferred to a crucible, oven-dried, weighed, ignited, and reweighed to provide estimates of dry weight and ash-free dry weight of plankton per liter in the concentrated samples.

In experiments using natural population densities, a sample of lake water was distributed among the series of bottles and exposed to natural light at various depths for 6 hours (9:00 a.m. to 3:00 p.m.). In experiments using filtered lake water, the water which had passed through No. 25 bolting cloth was treated in similar fashion.

The studies under completely natural conditions were made by determining pH of surface samples collected from the bay near the laboratory at intervals during the day and night, and computing CO_2 change in the natural water from the observed pH change during a given time interval. In the study of unconcentrated populations, the photosynthesis and respiration rates were computed as μmoles per liter of lake water per unit of time.

Respiration rates of bottom fauna were measured by collecting living specimens, placing them in a measured volume of water for a measured time interval, determining the pH change and computing CO_2 change per unit of wet weight of animals. These measurements were always made at the temperature of the natural water; the bottles containing the organisms were suspended in the lake during tests.

Light intensity at different depths was measured, near the midpoint of each test period, using a Weston photronic cell. The cell was enclosed in a watertight case with a clear glass window facing directly upward, it yielded a current of about 10 milliamperes at the surface on the clearest summer days, and the microammeter used could detect currents as small as one microampere. A current of 6.5 milliamperes corresponds approximately to a radiant energy supply of 1 g. cal. per cm.^{2} per min., as measured on the continuous-recording pyrheliometer maintained at the laboratory. The Weston photronic cell shows maximal sensitivity to yellow light and is relatively insensitive to wave lengths below 300 and above 700 millimicrons. Thus, it excludes much of the infrared, which comprises about 43 per cent of radiant energy on clear days, but which is not used in photosynthesis and it includes the wave lengths which are effective in photosynthesis (Rabinowitch 1951, Chap. 30) and which penetrate most readily into the aquatic environment (James and Birge 1938). In spite of this selective sensitivity, the relationship between photosynthesis and light intensity on cloudy days was significantly different from that on clear days.

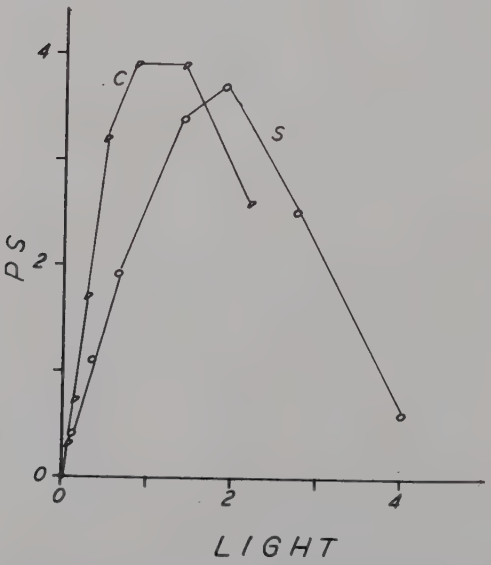

FIG. 2. Photosynthesis (µmol. CO_2 absorbed per 10 µl. of plant matter per hr.) vs. light (milliamperes, Weston photronic cell). Curve (C) was obtained on a cloudy day, (S) was obtained with the same sample on a sunny day.

In Figure 2, two curves are shown, obtained with the same plankton catch, studied on a cloudy day (C) and on a sunny day (S). The maximal photosynthetic yield in cloudy weather was obtained at a light intensity of about 0.8 milliamperes, while the same light intensity in clear weather showed a photosynthetic yield of only one-half the maximum, which was observed at about 2 milliamperes. This distinction was observed on several other occasions. It suggests that the light transmitted through cloud cover has a larger fraction of photosynthesis-supporting energy than light on a clear day. In the data presented below no distinction is made between experiments on clear and cloudy days. The photosynthesis vs. light curves presented below, therefore, are composite curves including clear, partly cloudy, and cloudy days. The data below which are expressed as micromoles per unit of plant volume can be converted, approximately, to gravimetric units by noting that a micromole represents 44 micrograms of CO_2 and that the mean ratio of ash-free dry weight to phytoplankton volume amounts to 0.31 mg./µliter (Verduin 1954).

RESULTS AND DISCUSSION

Experiments with concentrated populations

Figure 3 presents two composite curves of photosynthesis against light intensity. One curve (A) represents all data obtained during the autumn months. The other (S) represents all data obtained during spring months. The average maximal yield during the autumn months was about 5 µmol./10 µl./hr., and it occurred at a light intensity representing about one-fifth of full sunlight. Severe inhibition was evident at surface light intensities. The average maximal yield during spring months was about 4 and this curve has a broad plateau extending from one-fourth to three-fourths of full sunlight. Inhibition at surface light intensities was less severe. It appears that the communities which arise under the relatively poor light supplies of autumn use dim light more efficiently, and are more severely inhibited by bright light than the spring communities. Riley (1941) in his studies of oxygen production by phytoplankton on Georges Bank included measurements (his Table II) which permit conversion of his rates per m.^{3} and his plant pigment quantities to the units used here. The average rate for six cruises amounted to 6 µmol./10 µl./hr. In his experiments, natural population densities were used, and the samples were exposed for 24 hours.

In Figure 4 (upper curve) a graph of photosynthesis at optimal light intensities, against environmental temperature, is presented. Each point

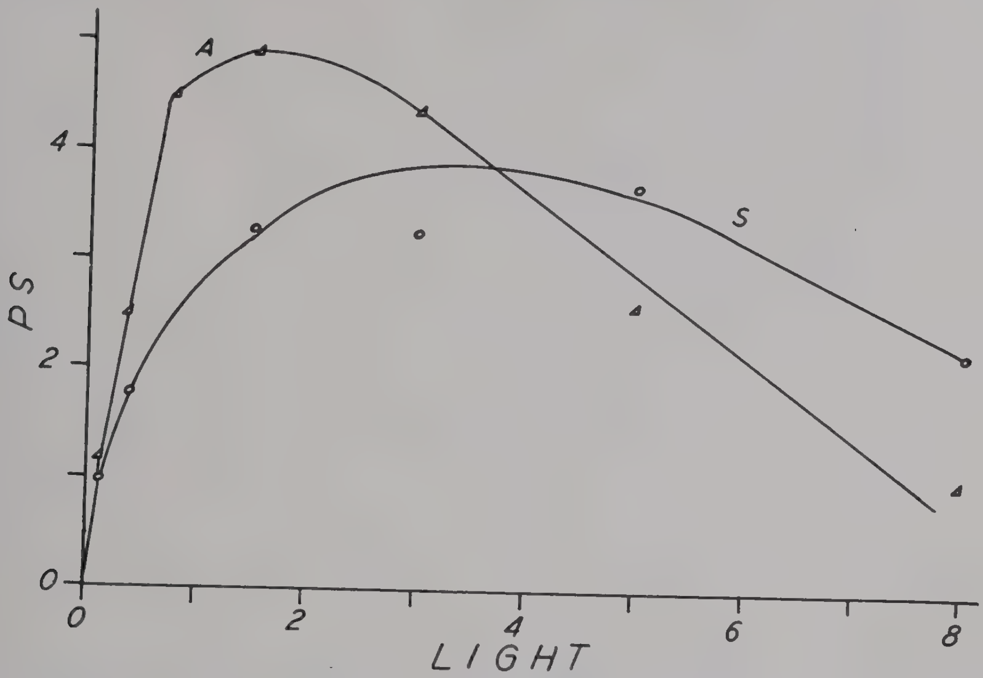

FIG. 3. Photosynthesis (µmol./10 µl./hr.) vs. light (ma., Weston cell). Curve (A) represents all data (33 series) obtained during autumn months, (S) represents all spring data (46 series).

is the average of 10 or more tests made near the environmental temperature indicated on the abscissa. The most striking feature of this graph is the high photosynthetic yield in cold water. It appears that natural communities living in a 0° to 3° environment show as high a rate of photosynthesis per unit of plant volume as do the communities living in 18° to 23° water. Riley observed his highest photosynthesis yields in cold water. In the April cruise, his average yield amounted to about 15 µmol./10 µl./hr., and water temperature was near 3° C.

A distinct depression is evident in Figure 4 near 10° C. Some exceedingly low values (one as low as 0.3) contributed to this average. It may be that senile communities, relict from the cold water environment in spring and from the warm water environment in autumn, are encountered in this temperature region.

In Figure 4 (lower curve) a similar graph of respiration rate against temperature is presented. The average values lie fairly close to a straight line, suggesting a positive correlation with temperature, with the exception of the 0° to 3° value which lies distinctly above the line.

Figure 5 is a graph of the photosynthesis rates at optimal light intensity against respiration rates for the same samples. The points represent individual tests, and three lines are drawn on the graph, one indicating the maximal ratio observed, a 20-fold excess of photosynthesis over respiration, one indicating the average ratio of 8, and one the minimal ratio of 1.5 in which photosynthesis at optimal light intensity barely exceeds the respiration rate of the population retained by No. 25 bolting cloth. The scatter diagram shows the variation observed in photosynthesis (0.3 to 14) and respiration (0.03 to 1.7) rates. It should be noted that plankton concentrations like those used in these experiments contain bacteria and zooplankton which contribute to the respiratory activity. The magnitude of this contribution is not known. It is interesting to note, however, that Ryther (1955) using pure cultures of a marine *Chlamydomonas* found that 28-day-old cultures exhibited photosynthesis rates just equal to respiration, and that 2-day-old cultures showed photosynthesis rates exceeding respiration by a factor of 12. A graph of photosynthesis against respiration for randomly selected cultures of various ages would closely resemble Figure 5.

The samples used in my experiments with concentrated populations were collected over a large area in western Lake Erie. In Figure 6, the photosynthesis rates at optimal light (upper number) and the respiration rates (lower number) are

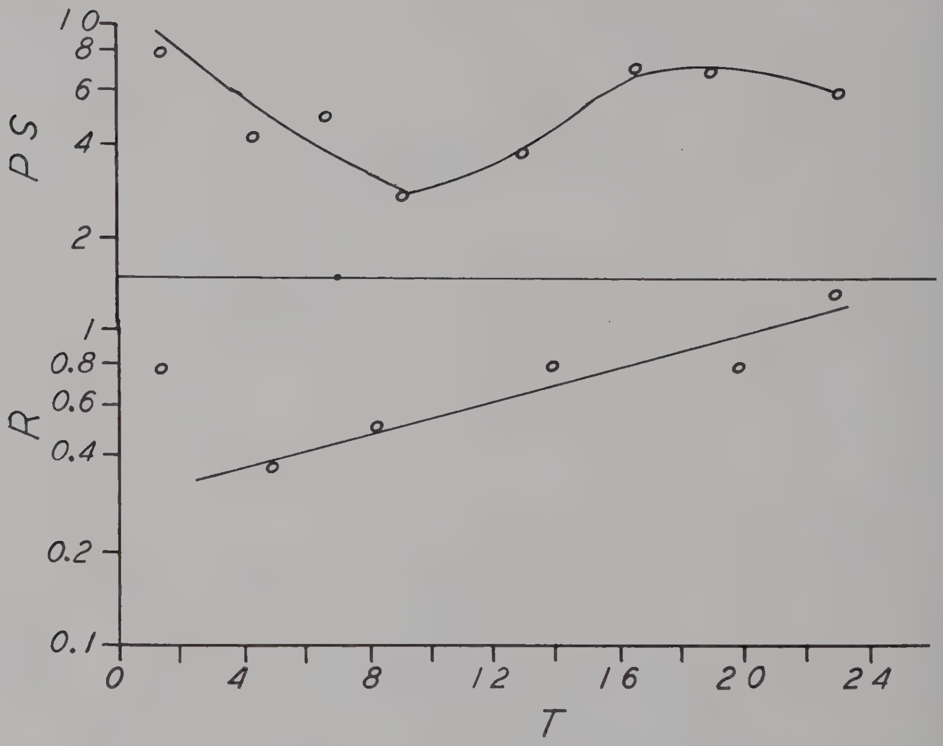

FIG. 4. Photosynthesis at optimal light intensity and respiration (both as µmol./10 µl./hr., on a log. scale) vs. environmental temperature (deg. C., linear scale). Each point is the average of 10 or more observations within ±2° of the temperature indicated on the abscissa.

averaged for different regions in the western basin. Collections from the region northwest of the Bass Islands exhibited higher photosynthesis (6.5) and respiration (0.85) rates than collections from other parts of the lake. In a previous paper (Verduin 1954), evidence of a convergence of water masses in this region was presented. It may be that the mixing of different waters creates conditions which support higher metabolic activity than in the more uniform waters of other regions.

The determinations of ash-free dry weight which were routinely made on the above samples permit computation of photosynthesis rates on that basis. The average photosynthesis at optimal light amounted to 1.6 µmol./mg. ash-free dry wt./hr. Riley's (1941) data can also be computed on this basis, amounting to 1.3 µmol./mg./hr. Jackson and McFadden (1954) obtained rates at optimal light intensity amounting to about 2 µmol./mg./hr. Their natural population densities were as high as my concentrated populations. It appears that phytoplankton from these widely divergent habitats show approximately the same average photosynthesis rate per unit of plant matter.

Experiments with natural population densities

Populations which have been concentrated with bolting cloth represent only a fraction of the total population. Experiments were begun in 1953 to estimate the magnitude of the fraction escaping the bolting cloth filter. Table II presents a comparison of the photosynthesis rate per liter in filtered and unfiltered water samples. This table shows that water which has passed through bolting cloth exhibits a considerable amount of photosynthetic activity. The average yield for the filtered samples was about 65 per cent of the average yield for natural water. Thus it appears that the bolting cloth retains, on the average, about one-third of the autotrophic community. The identity of the organisms which pass through bolting cloth is not known.

The data presented up to this point were obtained by enclosing samples in clear and blackened bottles. Although the test periods were short, the possibility remains that enclosure in bottles represents a large departure from natural conditions, and that data so obtained diverge widely from the

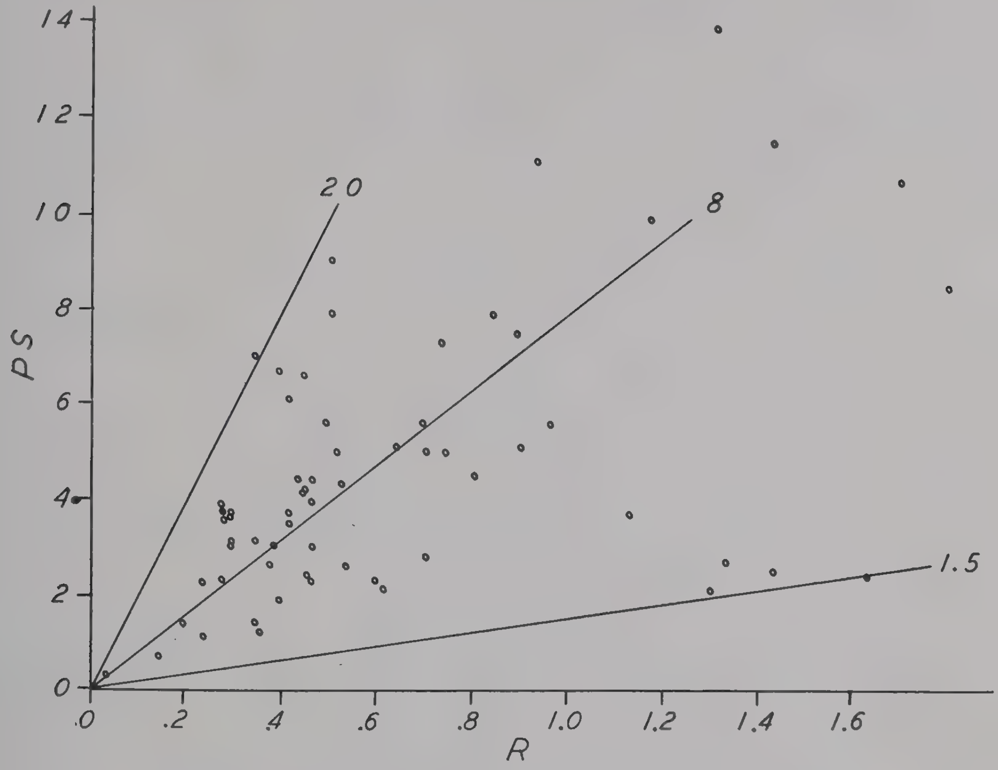

Fig. 5. Photosynthesis at optimal light intensity vs. respiration (both as µmol./10 µl./hr.). The maximal ratio of photosynthesis to respiration was 20, average was 8, minimal was 1.5.

Table II. Photosynthesis (µmol./1./hr.) at optimal light intensity, comparison of natural water and filtered water in bottles

Season	Natural water	Water filtered through No. 25 bolting cloth
Summer, bolting cloth fraction >3µl./liter ..	6.6	2.7
Summer, bolting cloth fraction <3µl./liter ..	4.4	4.1
Autumn................	3.6	3.6
Winter.................	0.6	0.3
Spring.................	3.3	1.3

rates occurring under completely natural conditions. Therefore, the measurement of photosynthesis and respiration under completely natural conditions was undertaken. The bay in front of the research laboratory is about 3 meters deep and a study of currents in the bay (Stansbery, D. H., unpublished data) showed that even in calm weather the flow through the bay renews the water at least once per day. Thus samples drawn from the bay have moved in from neighboring, and deeper, parts of the lake within a matter of hours. Samples drawn from the end of the dock in front of the laboratory at 3-hour intervals showed a distinct pH rise during daylight hours, followed by a decline during hours of darkness. Typical curves, obtained in summer, are graphed in Figure 7. The daytime pH rise at that time of year amounted to about 0.5 units, and the decline during the night usually brought the pH value back to approximately the value observed on the previous morning. These changes are large enough to provide reliable estimates of CO_2 change under completely natural conditions. This type of study has been continued for 10 to 15 days each month from July 1954 to January 1955, providing data at natural temperatures ranging from 23 to 0° C. In Figure 8, the CO_2 change per liter per day is graphed against environmental temperature. Each point represents the average of 10 or more days when water temperatures were within ±2° of the value indicated on the abscissa. When plotted on a semi-log graph a linear relationship between temperature and photosynthesis is obtained. In the warm waters of summer, the average daily

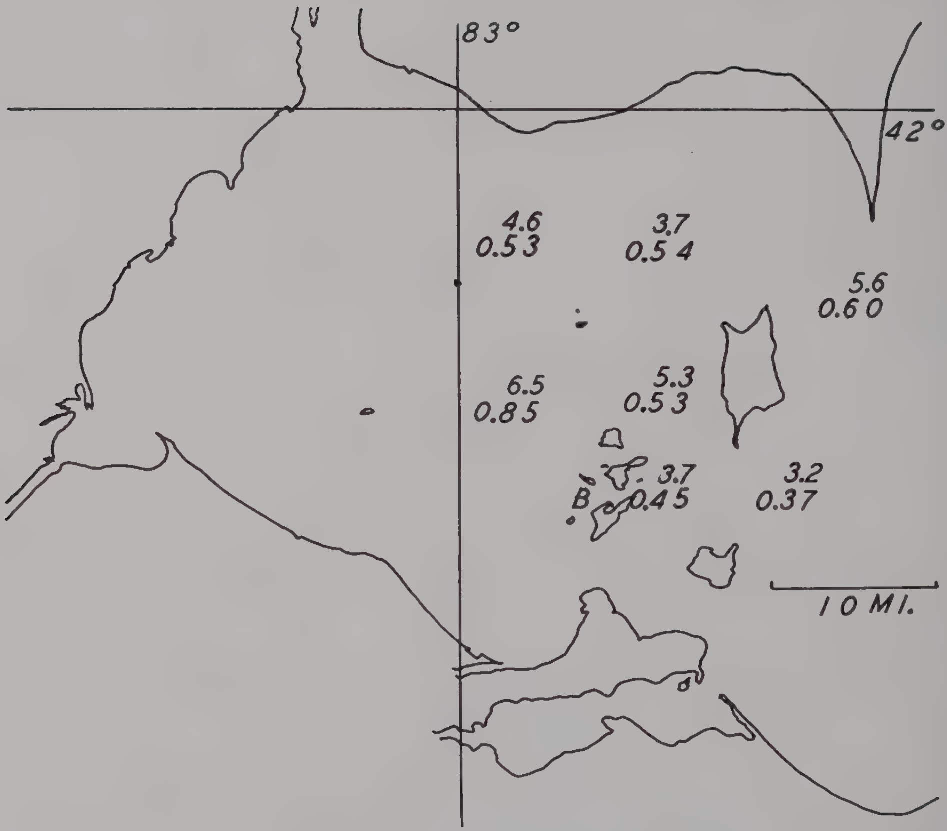

FIG. 6. Photosynthesis at optimal light (upper number) and respiration (lower number) (both as µmol./10 µl./hr.) associated with collections from different parts of western Lake Erie. Each value is the average of 10 or more collections from the region indicated. B identifies the Bass Islands.

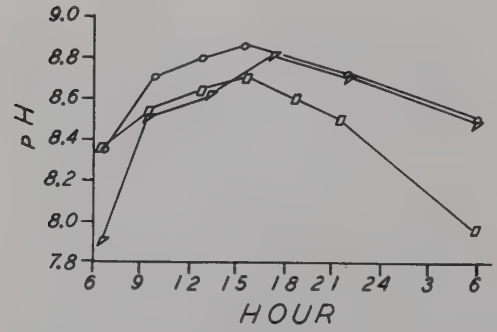

FIG. 7. Observed pH values in natural water samples collected from the bay in front of the laboratory, graphed against time of collection.

CO_2 uptake amounted to 68 µmol./liter. In winter, when water temperatures were near 0°, it was about 10 µmol./liter. In this graph, the combined influence of temperature, day length, and light intensity upon the magnitude of standing crop, and upon its metabolic rate, is portrayed. Note the difference between this graph and the upper curve in Figure 4.

Rates of photosynthesis and respiration per m² of water

The measurements of pH change under completely natural conditions can be used to provide estimates of photosynthesis and respiration per unit of water area. In the computations presented below the following assumptions are made: (1) that the pH rise observed during the day represents CO_2 change at optimal light, (2) that the relationship between light intensity and CO_2 absorption under completely natural conditions is like that observed when natural water samples were enclosed in bottles exposed at different depths, *i.e.,* the average rate of CO_2 absorption in the zone

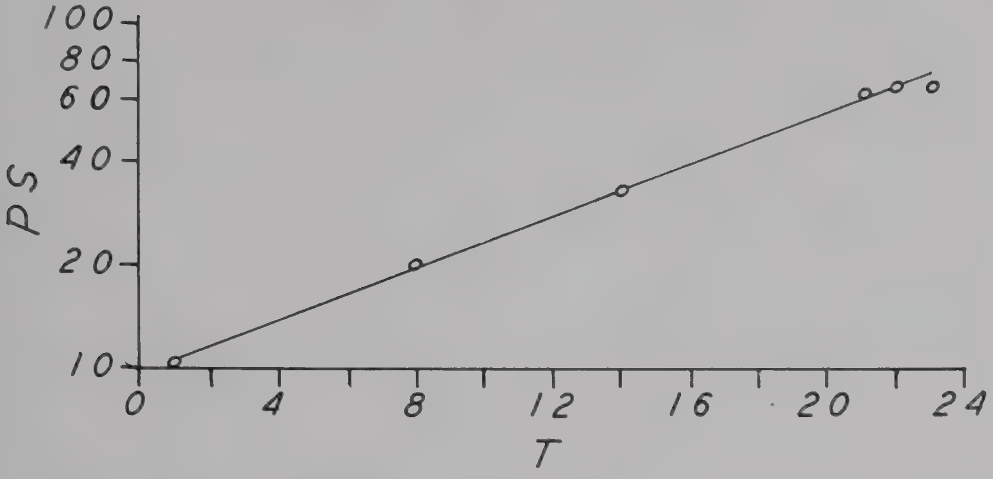

FIG. 8. Photosynthesis under completely natural conditions (µmol. CO_2 absorbed per liter of water per day) vs. environmental temperature (deg. C.). Each point is the average of 10 or more days when temperature was within ±2° of the value indicated on the abscissa.

lying above one per cent of surface light intensity amounts to 65 per cent of the rate at optimal light, and (3) that photosynthesis at light intensities lower than one per cent of surface light is negligible. These assumptions make the estimate a conservative one, (1) because whenever water in the bay is displaced by water from a deeper part of the lake the observed pH changes approach values at average, rather than optimal, light, and (2) because the observed pH rise represents photosynthesis in exces of respiration, rather than total photosynthesis. The depth associated with one per cent of surface light is usually about 5 meters, (Verduin 1954) in the region of the Bass Islands, thus the daily photosynthesis per square meter under summer conditions amounts to about:

$$\overset{(\text{mmol./m}^3\text{/day})}{68} \times \overset{(\text{avg. in phot. zone})}{0.65} \times \overset{(\text{m. in phot. zone})}{5} = 220 \text{ mmoles}$$

of CO_2 absorbed. It is worth noting that if the summer values for natural water in bottles (Table II) are averaged, the daily yield per cubic meter, assuming a 12-hour day, amounts to 66 millimoles or a yield of 215 mmol./m.²/day. This agrees closely with the measurements under completely natural conditions. The average yield for the July to January period, computed from data in Figure 8, amounted to 140 mmol./m²/day.

In observations under completely natural conditions, the importance of CO_2 exchange between water and atmosphere must be evaluated. If water has a free CO_2 concentration lower than that at equilibrium between water and air, then CO_2 will be gained, if higher, it will be lost. It is the time rate of gain or loss per unit area that concerns us. Romell (1927) cites Bohr's measurements of the evasion coefficient for CO_2 across the air-water phase boundary, quoting a value of 0.0023 cm./sec. at 15° C. I have made measurements using Lake Erie water, and obtained similar values. At 15°, the invasion and evasion coefficients for CO_2 are practically equal (the Bunsen coefficient is actually the ratio of invasion to evasion, and has a value of 1.019 at 15°) therefore the above value can be used to compute the CO_2 gain or loss if the difference between free CO_2 concentration in water and air is known. For example, if there were no free CO_2 in water, the CO_2 gain could be computed as

$$\overset{(\mu\text{mol. } CO_2 \text{ per cm.}^3 \text{ in air})}{0.013} \times \overset{(\text{invasion coefficient})}{0.0023} = 3 \times 10^{-5}\ \mu\text{mol./cm.}^2\text{/sec.}$$

or 26 mmol./m.²/day. This estimate represents the highest possible CO_2 gain from the atmosphere under natural conditions. The daily photosynthetic yields estimated above amount to about 200 mmol./m.² Thus, the highest possible gain from the atmosphere would contribute only one-eighth to the observed daily CO_2 change. The average CO_2 concentration difference between water and air is less than assumed in the above computation, hence gain from the air can be neglected without introducing an important error. Because the evasion coefficient for CO_2 is similar to the invasion coefficient in magnitude, and because the concentration differences in this direction, when they occur, are usually small, the CO_2 loss to the air also can be neglected. These computations indicate that the air-water phase boundary is a remarkably effective barrier to CO_2 exchange (*cf.* Spoehr 1926: 45). The close agreement between the diurnal pH rise and the nocturnal pH decline under natural conditions, therefore, is evidence that photosynthesis of the autotrophic community is practically equal to respiration of the total community in western Lake Erie. Riley (1941) in his computations of O_2 production per m.^{2} on Georges Bank lists values exceeding O_2 consumption by about 15 per cent (avg. of 6 cruises, computed from his Table VI) indicating a rather close agreement between photosynthesis and respiration in that environment also. The work of Jackson and McFadden (1954) in Sanctuary Lake indicated a similar balance between photosynthesis of the autotrophic community and respiration of the total community. The relatively slow rate of CO^2 exchange across the air-water phase boundary makes the aquatic environment approximate a closed system with respect to CO_2 supply. It seems that the processes of photosynthesis and respiration in the aquatic environment approximate a steady state relationship in which the CO_2 utilized in photosynthesis is produced by respiration and the O_2 utilized in respiration is a product of the photosynthesis reaction. There are times, however, when a pronounced excess of photosynthesis over respiration may be observed. At such times a distinct rise in pH level occurs, and values as high as 9.1 have been observed in western Lake Erie, although the values routinely observed lie between 7.9 and 8.7. Conversely, there are periods when respiration exceeds photosynthesis, and pH levels as low as 7.6 have been observed. These pronounced departures from the approximate steady state described above have not been studied adequately, so no reliable statements about their frequency of occurrence and their rates of change can be made.

Riley's estimates of total O_2 production per m.^{2} per day varied from 9 mmoles in January to 330 in April. The average for 6 cruises was 126, thus is similar to the average of 140 for western Lake Erie. The data of Jackson and McFadden can be used to compute the yield per m.^{2} In that shallow habitat (1.5 m.) the daily yield amounted to 210 mmoles. Gessner's (1949) data for Wesslingsee can also be used to obtain an approximate yield per m^2. In his table on page 383 the O_2 concentrations indicate that the euphotic zone extended to about 2.5 m. He reports chlorophyll determinations averaging about 50 µg./liter (his Fig. 7) and photosynthesis yields under optimal light amounting to about 10 µg. CO_2 absorbed per µg. of chlorophyll per hour, or about 0.23 µmol./µg./hr., which would represent a yield of 140 µmol./liter of water/day. Assuming that the average yield in the euphotic zone is 65 per cent of the yield at optimal light, an estimate of

$$\begin{array}{ccccc} \text{(mmoles/m.}^3\text{/day)} & & \text{(avg. in phot. zone)} & & \text{(m. in phot. zone)} \\ 140 & \times & 0.65 & \times & 2.5 = 230 \text{ mmoles/m.}^2\text{/day} \end{array}$$

is obtained.

The highest daily yields per m.^{2} reported by Manning and Juday (1941), in their study of several Wisconsin lakes in summer, amounted to 150 mmoles for Scaffold Lake. The average yield at maximum depth (7 lakes) amounted to 75 mmoles. In those lakes the euphotic zone extended into the hypolimnion, and Manning and Juday assumed that yields per unit chlorophyll below the thermocline were one-third as high for a given light intensity as yields above the thermocline (this assumption was based on experiments with collections from deep water).

The above comparisons indicate that in eutrophic waters whose euphotic zone is confined to the epilimnion, the daily photosynthetic yield is of the order of 200 mmol./m.^{2} This value is similar to that reported by Steemann-Nielsen (1954) for the most productive ocean regions (3 g. C/m.^{2}/day, or 250 mmoles), in the least productive areas he reports values of 0.05 g. (4 mmoles). In the terrestrial habitat, alfalfa, under optimal conditions, yields about 10 times as much (18 µmol./cm.^{2}/hr., Verduin 1953). Gessner (1949) estimates that the maximal yields in the aquatic habitat are equal to those in the terrestrial habitat. He bases this estimate on the observation that in both habitats the maximal chlorophyll concentrations per square meter are alike (1 to 2 g.) and that photosynthetic yields per unit chlorophyll at optimal light intensity are alike (10 g. CO^2 absorbed/g. of chlorophyll/hour). His estimate of maximal yield then assumes that all the chlorophyll beneath a square meter is exposed to optimal light intensity. In the terrestrial habitat this condition is frequently met, but in the aquatic habitat only a small fraction of the chlorophyll is in the optimally lighted zone, therefore the maximal yields postulated by Gessner for the aquatic habitat are not likely to be observed under natural conditions.

Estimate of respiration of bottom organisms

In western Lake Erie, the major components of the bottom fauna are mussels (78 per cent) and insects (16 per cent) yielding an average wet weight of 85 grams per square meter (mussel shell excluded).[3] Respiration rate determinations using such organisms at environmental temperature show that at 23° the aquatic insects exhibit rates of about 20 μmol. CO_2/g./hr., the mussels exhibit rates of about 1, and that as the water cools the rates are reduced by approximately a factor of 2 for each 10° interval. At summer temperatures, the daily respiration per square meter would be about

$$[(85 \times 0.78 \times 1) + (85 \times 0.16 \times 20)] \times 24 = 8 \times 10^3 \ \mu\text{moles},$$

or about 4 per cent of the total daily energy flow per square meter. The reduced rates in cooler water would approximately match the reduction in total rates evident in Figure 8, therefore the bottom fauna probably contribute about 4 per cent on the annual basis also. This estimate includes only the macroscopic animals. The respiration of microbial fauna and flora inhabiting the bottom has not yet been estimated.

SUMMARY

Measurements were made of photosynthesis and respiration in natural communities of western Lake Erie, using pH change in natural water as an index of CO_2 change. Photosynthesis vs. light curves showed that autumn communities use dim light more efficiently than do spring communities. Photosynthesis rates, per unit of plant volume, exhibited by communities collected from, and tested in, 0° water were as high as those of communities collected from, and tested in, 23° water. The ratio of photosynthesis at optimal light to respiration showed an average value of 8, with values as high as 20, and as low as 1.5 being observed. Photosynthesis at optimal light showed average yields of 5 μmoles CO_2 absorbed/10 μl./hr., and 1.6 μmol./mg. ash-free dry wt./hr. These are similar to values computed from the literature for marine phytoplankton and for myxophycean communities in fresh water.

Filtering lake water through No. 25 bolting cloth removed about one-third of the photosynthetic activity, thus two-thirds of the autotrophic community remains unidentified. Measurements of photosynthesis under completely natural conditions indicated an average yield of 68 μmol. CO_2 absorbed/liter of water/day at 23°, falling off at cooler temperatures to 10 at 0°. It is shown that CO_2 exchange between water and air is negligible in comparison to the daily CO_2 changes within the aquatic environment. It appears that photosynthesis of the autotrophic community and respiration of the total community are approximately equal.

The rates of photosynthesis per square meter per day amounted to about 220 millimoles at summer temperatures, and averaged 140 for the July-January period. These values are similar to estimates for other eutrophic waters computed from the literature. Measurements of respiration rates of bottom fauna, combined with a knowledge of the weight of animals per square meter yielded an estimate indicating that they contribute about 4 per cent to the total respiration per square meter of water.

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BREEDING BIRD POPULATIONS IN RELATION TO PLANT SUCCESSION ON THE PIEDMONT OF GEORGIA

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Ecological succession, or the orderly change and development of biotic communities and the ecosystems of which they are a part, is one of the important principles of ecology. Plant succession has been subject to much investigation since 1900, but animal succession is less well-known, studies of it being mostly qualitatively descriptive. Due to the great mobility of animals and the general lack of knowledge dealing with taxonomy and life histories of a large part of the fauna, animal succession in terrestrial communities is more difficult to study than plant succession. At present, the most profitable line of approach is to select for study some significant part of the community or a "population" composed of species groups for which good census methods have been worked out. In terrestrial communities, birds are usually conspicuous components, and the territorial behavior of many species makes possible relatively accurate field determinations of population density during the breeding season. Furthermore, community selection by birds is most pronounced during this critical period in their life history. Since animals, as well as plants, may be active agents in bringing about community changes, quantitative data on population size should help in the understanding, prediction, and control of the changes which we designate as "ecological succession."

The present paper deals with the breeding bird populations of areas representing seral stages in secondary succession on the upland of the Piedmont physiographic region. A similar study in the Mountain region has been published (Odum 1950) and one for the Coastal Plain is in progress. For aid in the location and botanical description of study areas we are indebted to the following: Dr. Wilbur H. Duncan, Dr. Don L. Jacobs, Department of Botany, and Dr. L. W. R. Jackson, School of Forestry, University of Georgia; Dr. Catherine Keever, State Teachers College, Millersville, Pennsylvania; and Mr. Jack Brown, Soil Conservation Service, Athens, Georgia.

Plant Succession on the Piedmont

The dynamics of plant succession on the Piedmont have been well-monographed by Oosting (1942). The major stages in the upland sere are diagrammed in Figure 1. Abandoned cotton, corn, and other "row crop" fields are usually dominated by crabgrass (*Digitaria sanguinalis*) and horseweed (*Leptilon* [*Erigeron*] *canadense*) during the first growing season following cessation of cultivation. The horseweed does not reach its full height (3-6 feet) until late summer; during the bird breeding season, the plants are usually less than a foot high. The second year, aster (*Aster pilosus* L.) and/or ragweed (*Ambrosia artemisiifolia*) become dominant, although crabgrass and stunted horseweeds are usually present as an understory. By the third year broomsedge (*Andropogon virginicus* and several less common species of the same genus) seeds in and may form a continuous cover in a few years. Pine seedlings (*Pinus taeda* and *P. echinata*) may appear in the broomsedge fields by the third year, and these pines may form a closed canopy in 10-15 years. Usually, however, a mixed shrubland of pine seedlings, blackberries (*Rubus*), sumac (*Rhus*), plum (*Prunus*) and other deciduous shrubs and small trees share dominance with broomsedge for a period before the pines take over. Since most cropland in the Piedmont is terraced, and since vegetative succession has a head start on the terraces, grassland-shrubland combinations are common in the early years. As the pines mature, they are unable to reproduce under their own shade,

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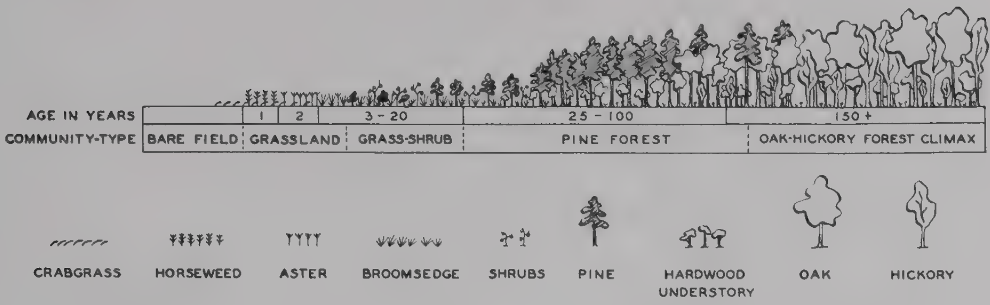

Fig. 1. Schematic diagram of secondary succession on the Piedmont region (after Odum 1953).

but deciduous saplings can develop under the pine canopy. Consequently, by the time the pine stand is 40 or 50 years old, a distinct understory of hardwoods has frequently developed. At 70 or 80 years, some pines begin to drop out. Hardwoods, on the other hand, especially oaks and hickories, steadily increase to equal the pines in size, and eventually after 150 or more years these hardwoods become dominant or climax, leaving only a few scattered pine relics. Hardwood, but not conifer, reproduction is quite evident in such a climax forest.

Methods

A total of 13 areas each approximately 20 acres in size were studied, each consisting of as uniform a habitat as could be located. Ten of the areas represented successive stages in natural succession from one-year abandoned fields to a young climax forest. Three areas of cultivated grasslands (pastures, etc.) were included for comparison with natural grasslands. Eleven of the areas were censused in 1950 and two in 1951. Two of the forested areas had also been censused prior to 1950 (Odum 1947a, 1947b) and these earlier results were averaged with those of 1950 to obtain a population estimate for the seral stage represented.

Censusing was accomplished by the territory-mapping technic as employed by Williams (1936, 1947), Kendeigh (1944) and by Odum in the aforementioned studies. This census method is most accurate for birds holding "type A" territory as classified by Nice (1941), *viz.,* the defended area used for mating, nesting, and feeding ground for the young, with the result that adult birds remain within a restricted area for an extended time. Fortunately, the large majority of birds (including most passerines) of the upland communities have this type of territory. Final density estimates for each area were based on a minimum of 5 early morning census visits (between 5 and 10 A.M.) made at a one-week or 10-day intervals during the critical breeding months of April, May, and early June. A census visit to a forested plot usually required at least 3 hours whereas field communities could be covered in 2 hours or less. If a territory proved to be partly outside the study area, the appropriate fraction which was inside was used in totaling the density of the species in question. All density figures represent the actual number of *occupied* territories per 100 acres, which number becomes the *estimated* number of pairs per 100 acres, assuming that both a male and a female occupy a territory sometime during the season. Species with territories or home ranges averaging as large or larger than the study area (for example, the mourning dove or hawks) are indicated in the tables by "plus" signs even when their nests were actually on the study areas. Such birds are definitely a part of the population of the study areas, but their actual "space-relative" densities obviously cannot be determined when sample areas are small in relation to home range. Censusing larger and more wide ranging species becomes almost an individual problem with each species and is beyond the scope of this paper. Species and individuals which were observed to visit the study areas occasionally for feeding purposes only, but which were not believed to include the area or any part of it in their regular breeding territories, were regarded as "visitors" and are not included in the tables.

The Study Areas

The study plots may be conveniently classified as (1) grassland, (2) grassland-shrubland, (3) pine forest, and (4) hardwood forest. For each of the 13 areas listed below, the size of the plot, the year in which it was censused, and a brief description of the plant community are given. Transects and quadrats were used to determine the quantitative as well as the qualitative distribution of plants. Botanical nomenclature is taken from Blomquist and Oosting (1948) and Small (1933). All of the areas are located within 20 miles of Athens, which lies approximately in the middle of the Georgia Piedmont at an average elevation of 700 feet.

A. Grassland

1. One-year field. 1951. 20 acres. In cotton in 1950, last cultivated in July of that year. In May, 1951, dead cotton stalks were still standing (providing singing perches for grasshopper sparrows). Crabgrass formed a fairly heavy ground cover, especially along the rows of old cotton plants. Horseweeds, dominant in fall, were 4-6 inches high and well-distributed all over the field. The field was level without terraces. It was bounded on one side by a road, on another by an abandoned house and yard, and on the other sides by low hedgerows and plum thickets.

2. One-year field. 1951. 20 acres. In corn in 1950. Adjoins area No. 1 but on more sloping terrain. Three terraces covered with Johnson grass (*Sorghum halepense*) cross the field. Most of the previous year's corn stalks were still standing (and were used as song perches). Distribution of crabgrass and horseweeds very similar to area No. 1.

3. Three-year field. 1950. 20 acres. This field was bordered by pine woods, cultivated fields, and a young oak-hickory-pine tract. It was nearly level, containing only one low terrace on which grew five small black gums (*Nyssa sylvatica*) and a pine seedling. Sheet erosion was apparent in some places but there was no evidence of fire. In one part of the field small (4-10 inches) horseweeds were most numerous with an admixture of first year broomsedge, dock (*Rumex hastatulus*), aster, isopappus (*Isopappus divaricatus*), and lespedeza (*Lespedeza stipulacea*). In another part, broomsedge was dominant with much rabbit-tobacco (*Gnaphalium obtusifolium* and *G. purpureum*), dock, aster, lespedeza, and isopappus forming a thick herbaceous cover.

C–1. Oat field. 1950. 18 acres. Located on the University of Georgia Dairy Farm and maintained by its personnel. This field of oats (*Avena sativa*) was bordered on one side by a stream and thicket, on another by a road, and by permanent pastures on the other two sides. There was some terracing, but plants on the terraces, including oats, corn cockle (*Agrostemma githago*), thistle (*Cirsium* sp.), and cow vetch (*Vicia cracca*), did not form a denser cover than that of the over-all character of the field. This field was mowed and raked on May 19, 1950, censuses being taken before and after this date.

C–2. Temporary pasture. 1950. 18 acres. This pasture was seeded September 1, 1949, with the following mixture per acre: rye grass (*Lolium* sp.), 40 lbs.; crimson clover (*Trifolium incarnatum*), 20 lbs.; and oats, 3 bu. No terraces were present. Fences and small wooden enclosures provided song perches. It was grazed at night from October 20, 1949, until after the present study. Cows came into the field about 5 P.M. daily, and the average was 2.75 cows per acre. Except for this grazing, the field was undisturbed during census operations.

C–3. Permanent pasture. 1950. 18 acres. This pasture was adjacent to the oat field, the two being separated by a fence and small road. It was seeded Sept. 20, 1949, with the following mixture per acre: Ladino clover (*Trifolium repens*), 3 lbs.; Kentucky 31 fescue (*Festuca elatior arundinacea*), 8 lbs.; orchard grass (*Dactylis glomerata*), 7 lbs.; and it contained scatterings of thistle and cow vetch. A few small terraces provided additional cover for birds, and inverted culverts, small enclosures, and fences provided song perches. The area had been grazed lightly prior to March 1, 1950, but not since that time. It was mowed gradually between May 23 and 29, 1950.

B. Grassland-shrubland

4. Grass (90%)-shrub (10%) field. 1949. 20 acres. According to local farmers this field had been fallow for about 15 years. It was regularly terraced in its downward slope, and a transect revealed that the terraces covered 10% of the entire field. The terraces supported blackberry (*Rubus* sp.), wild plum (*Prunus americana*), young sassafras (*Sassafras albidum*) up to 6 feet in height, red sumac (*Rhus glabra*) 3 feet high, and a few young loblolly pines. Increment borings showed the age of these pines to vary between 5 and 10 years. The interterrace areas varied highly in species and abundance of plants due to gully erosion and burning 3 years previously, but generally speaking, broomsedge was the dominant plant. Other important plant constituents included daisy (*Chrysanthemum leucanthemum*), squaw-weed (*Senecio smallii*), cow vetch, beard-tongue (*Penstemon canescens*), dwarf five-finger (*Potentilla pumila*), daisy fleabane (*Erigeron ramosus*), goldenrod (*Solidago* sp.), cross-vine (*Bignonia capreolata*), wild carrot (*Daucus carota*), and Bermuda grass (*Cynodon dactylon*).

5. Grass (65%)-shrub (35%) field. 1950. 12.8 acres. The age of this abandoned field could only be estimated at 20 years from the age of the trees along the terraces. A transect showed that terraces and gullies with their accompanying woody plants covered 35% of the field. Terrace and gully cover included blackberry thickets up to 6 feet in height, red sumac 6 feet high, wild plum 10 feet, loblolly pines 15 years old, black gum 12

feet, hawthorn (*Crataegus* sp.), sweet gum (*Liquidambar styraciflua*) 20 feet, water oak (*Quercus nigra*), and tulip poplar (*Liriodendron tulipifera*) 25 feet, black cherry (*Prunus serotina*) 15 feet, and sassafras 7 feet. Blackberry and wild plum composed the bulk of the terrace plants, whereas the trees were scattered mostly along the gullies. Interterrace areas were dominated by broomsedge, but also contained squaw-weed, dock, wild lettuce, daisy fleabane, cross-vine, witch-grass (*Leptoloma cognatum*), panic grass (*Panicum* sp.), horseweed, and others. This field was bordered by pine woods, a stream thicket, and by an older field containing pines.

C. Pine forest

6. 25-year-old pine forest. 1950. 16 acres. This forest contained pines of various ages up to 20 years, making the ecological age of the area about 25 years. Shortleaf slightly outnumbered loblolly pines. Parallel transects showed that open, grassy plots comprised 44% of the entire study area, thickets 23%, and pines 33%. The open areas contained a variety of herbaceous and woody plants, but were dominated by broomsedge and cross-vine. Thickets were confined to old terraces and were composed mostly of blackberry and red sumac, but also contained scatterings of hawthorn, wild plum, black cherry, and black gum. The area was bounded by pine forests of various ages. There was no evidence of recent fire, but gully erosion was frequent.

7. 35-year-old pine forest. 1947. 24 acres. This study area was dominated equally by loblolly and shortleaf pines which ranged from 20 to 40 years old (Odum 1947a). Terraces remaining from previous cultivation supported a heavier undergrowth than did the interterrace areas. This understory consisted of tulip poplar, dogwood (*Cornus florida*), persimmon (*Diospyros virginiana*), sweet-gum, and water oak. Broomsedge was still present in some interterrace areas where it had not been shaded out by the pine canopy. A small stream crossed the northern boundary of the study area. It was bounded on three sides by a similar pine forest, but on the other side by bottomland hardwod forest. There had been no recent fire or other disturbance on this area.

8. 60-year-old pine forest. 1949 and 1950. 20 acres. According to the records of the University Forestry School, this forest was an abandoned field 50 years ago, thus making the age of the area —measuring from a fallow field to present—roughly 60 years. The entire area covered at least 50 acres; 20 acres of the most uniform part were censused. A transect showed that loblolly pine outnumbered shortleaf more than 2:1. The height of the forest was 60 feet. Loblolly pines averaged 5 in d.b.h., some trees exceeding 10 in. and one reaching 22 in. Shortleaf pines averaged 8.7 in. with a maximum of 14 in. A distinct understory of deciduous trees was present, especially along old gullies. It contained the following trees in order of decreasing abundance: sweet-gum, hawthorn, dogwood, black gum, black cherry, tulip-poplar, water oak, southern red oak (*Q. falcata*), and persimmon.

9. 100-year-old pine forest. 1950. 20 acres. This was part of an extensive pine forest located in Walton County, which had been relatively undisturbed until selectively lumbered in 1949 and 1950. The census area was in the least disturbed part available, but some of the large trees had been removed in 1949, leaving some slash and logging trails. There was no disturbance during the census period, and no evidence of recent fire. A transect showed that shortleaf pine outnumbered loblolly about 3:2, both of which averaged 13 in. d.b.h., maximum trees reaching 27 in. and 22 in., respectively. In addition to 23 mature trees counted along this transect, there were 5 stumps, indicating the degree of the selective lumbering. The height of the forest was 85-90 feet. The deciduous understory which was continuous and well-developed throughout the area, included, in order of decreasing abundance, sweet gum, dogwood, sassafras, persimmon, black cherry, water oak, and northern red oak (*Quercus borealis*).

D. Hardwood forest

10. Oak-hickory climax forest. 1947 and 1950. 20 acres. Except for the removal of relict pines, this area had been little disturbed for an estimated 150-200 years. Two small streams flowed through the area and joined at one end. The census area was elongate, embracing the larger of the two streams. One slope was gentle whereas the other was rather steep. A small strip of similar forest occurred all around the edge of the census area. Plant transect studies showed that hickories (*Carya* spp.), white oak (*Quercus alba*), and black oak (*Q. velutina*) predominated on the hillsides with a scattering of northern red oak, southern red oak, and red maple (*Acer rubrum*). Along the streams in addition to the above trees were also found beech (*Fagus grandifolia*), sweet-gum, tulip poplar, and silver bell (*Halesia carolina*). The mature trees averaged 18 in. d.b.h. with the larger oaks reaching 25-27 in. The height of the forest was 100 feet or more. The well-developed understory consisted of the seedling oaks and hickories, dogwood, hawthorn, sourwood (*Oxydendrum arboreum*), persimmon, and post

oak (*Quercus stellata*). A few old shortleaf pines were left standing in the area.

RESULTS

Results of the censuses are shown in Tables I and II and in Figure 2. Calculated densities in terms of pairs per 100 acres are rounded off to the nearest whole number. Species having territories too large for density estimates on the basis of 20-acre samples, as well as species with low calculated densities, are listed separately in Table I. Ornithological nomenclature follows the A.O.U. check-list.

Changes in population density and composition.—As may be seen from Table I and Figure 2, density increased as the grass and forb covered fields became invaded by shrubs and small trees, decreased with the coming of the young pine forest, and increased again as the hardwood understory developed in older pine forests. Thus, a trend toward population increase with succession from bare ground to the sub-climax or young climax was interrupted by low densities encountered in young pine forests. Changes in the number of species with ecological age of habitat paralleled changes in density except that there was little increase beyond the 60-year-old pine stage (Figure 2).

As is perhaps typical of successional series, it will be noted from Table I that most species have a very definite range of occurrence in the sere, but some persist through many stages involving most of the time period required to develop a climax. In this study, the cardinal (*Richmondena cardinalis*) and the towhee (*Pipilo erythrophthalmus*)

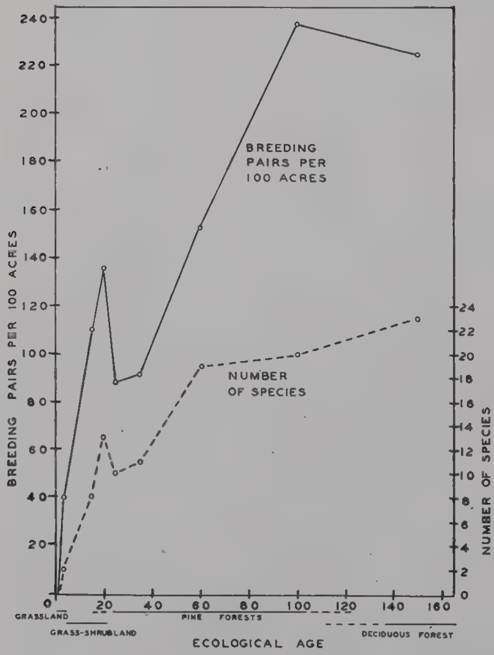

FIG. 2. Changes in density and number of species of breeding birds with advance of community development from abandoned agricultural fields to climax forest. Ecological age is in approximate years.

TABLE I. Breeding bird density in a secondary upland sere of Piedmont region of Georgia. Figures are occupied territories or estimated pairs per 100 acres*

Stage in succession:	Grass-forb		Grass-shrub		Pine forest				Oak-hickory climax
Age in years:	1	3	15	20	25	35	60	100	150+
Study Area No.:	1-2	3	4	5	6	7	8	9	10
Group A—Common species having density of 5 or more in some stage.									
Grasshopper sparrow	10	30	25						
Eastern meadowlark	5	10	15	2					
Field sparrow			35	48	25	8	3		
Yellowthroat			15	18					
Yellow-breasted chat			5	16					
Cardinal			5	4	9	10	14	20	23
Eastern towhee			5	8	13	10	15	15	
Bachman's sparrow				8	6	4			
Prairie warbler				6	6				
White-eyed vireo				8		4	5		
Pine warbler					16	34	43	55	
Summer tanager					6	13	13	15	10
Carolina wren						4	5	20	10
Carolina chickadee						2	5	5	5
Blue-gray gnatcatcher						2	13		13
Brown-headed nuthatch							2	5	
Blue jay							3	10	5
Eastern wood pewee							10	1	3
Ruby-throated hummingbird							9	10	10
Tufted titmouse							6	10	15
Yellow-throated vireo							3	5	7
Hooded warbler							3	30	11
Red-eyed vireo							3	10	43
Hairy woodpecker							1	3	5
Downy woodpecker							1	2	5
Crested flycatcher							1	10	6
Wood thrush							1	5	23
Yellow-billed cuckoo								1	9
Black and white warbler									8
Kentucky warbler									5
Acadian flycatcher									5
Group B—Less common species, or those whose density could not be determined by method used (presence indicated by "+")									
Bob-white			+	+	+				
Goldfinch				+					
Indigo bunting				4					
Catbird				4					
Mourning dove					+			+	
Chuck-will's-widow					+	+		+	+
Brown thrasher						4	+		
Blue-headed vireo							3		
Yellow-throated warbler							3		
Flicker								3	3
Pileated woodpecker								+	
Totals	15	40	105	127	83	95	163	237	224

*A condensed version of this table appeared in Odum (1953).

were found in the largest number of successive seral stages.

It seems probable that in very old or virgin hardwood forests, which do not now exist in the Athens region, breeding bird density would be less than in the fairly young climax oak-hickory area censused because the forest understory would likely be reduced by tree competition and shading. This would be particularly true on ridges away from streams or on other relatively dry sites. Accordingly, we may tentatively conclude that, for the Athens region, a peak in population density may be expected in the mature pine forests in which normal understory development has not been inhibited and in the more mesophytic young hardwood climaxes. Or, to put it another way, a peak in density may be expected in the late subclimaxes on moist sites.

Essentially, upland succession on the Piedmont involves four broad stages dominated by four distinct plant life forms which succeed one another, *i.e.,* herbs (grass and forbs), shrubs, pines, and hardwoods. Each of the four major stages—which we shall desigate as grassland, shrubland, pine forest, and hardwood forest—has its distinctive breeding bird species and apparently also characteristic densities.

The grasshopper sparrow (*Ammodramus savannarum*) and the meadowlark (*Sturnella magna*) are the only two common breeding birds of the Athens area (or indeed of most of the southeastern United States) which are true grassland species. Other species frequenting recently abandoned old fields require some shrubs or trees in their nesting territories, and hence were not found in large uniform one- and two-year sample fields (Nos. 1-3) except as visitors.

There are two southeastern species, the killdeer (*Chadradius vociferus*) and the horned lark (*Eremophila alpestris*) which feed and nest on bare or sparsely covered ground and hence would represent the pioneer species in a successional series beginning with bare ground. The killdeer is uncommon in the Athens area and prefers wet ground, while the horned lark, which is rapidly extending its breeding range eastward from the prairies, has not yet become well-established in Georgia where airports are usually the first "habitats" locally invaded. If the invasion trend continues, it seems likely that the horned lark will breed in the Athens region where its niche is unoccupied, and thus become one of the first successional species. In this connection, it is interesting to note that on the English heathlands, Lack (1933) found that closely grazed and partly bare turf as well as thin grass areas supported a good population of 6 species including the skylark (related to our horned lark), wheatear, lapwing, stone curlew, and meadow pipit. In the southeastern United States there is no comparable array of open-country birds, probably because, until recently, there was no suitable habitat. With increasing numbers of pastures and airports, it seems likely that a larger and perhaps more diverse bird population may develop in time on sparsely covered ground.

Though it was not the purpose of the present study to determine accurately the size of a species' territory, it was possible to obtain rough estimates of territory size. The two pairs of meadowlarks in field No. 3 each held territories of about 7 acres. The 6 grasshopper sparrow territories were much smaller, each consisting of one or two acres.

"One year" cultivated fields (C-1, C-2, C-3; see Table II), of course, have a denser plant cover than one year abandoned fields. These fields supported a two-species bird population similar to the two and three year natural field, but at a higher density. Actual ground cover was considerably thicker in the permanent pasture, which had a higher bird population as compared with the oat field and temporary pasture. Nests of grasshopper sparrows and meadowlarks were found on the two pasture areas, and were checked carefully. The permanent pasture was gradually mowed, and upon one occasion a grasshopper sparrow's nest was destroyed by the machinery. This pair did not leave the area, but remained to start a new nest.

TABLE II. Breeding bird density in cultivated grasslands. Figures are occupied territories (in round numbers) or estimated pairs per 100 acres

Study Area No.	C-1		C-2	C-3
Type of field	Oat field		Temporary pasture	Permanent pasture
	before mowing	after mowing (May 19)		
Grasshopper sparrow..	19	14	16	28
Eastern meadowlark..	—	—	11	11
Totals..........	19	14	27	39

The effect on birds of mowing was also noted in the oat field. After mowing on May 19, the breeding grasshopper sparrows decreased from 4 to 3 pairs. No actual nests or young were seen at any time in this field, but after mowing, birds continued to sing. The pair which disappeared from the mowed oat field did not move into the adjacent permanent pasture, C-3.

Changes occurring in transition between grassland and shrubland appear correlated with the appearance of the shrub life form since all the new species (not found in the pure forb-grass fields, areas Nos. 1-3) require bushes for nesting, song perches, or escape cover. The field sparrow (*Spizella pusilla*) and the yellowthroat (*Geothlypis trichas*) proved to be the two commonest species in the habitats with grass-shrub mixtures. It will be noted that grasshopper sparrows and meadowlarks maintained approximately the same density in the 10% shrub field (area 4) as was found in fields with no shrubs (areas 1-3), but these species all but disappeared when shrubs covered 35% of the field (as in area 5) even though over half of the total area still had a good grass cover.

Low density of breeding birds is a characteristic feature of young southeastern pine forests (25 to 60 years old) as is not only shown by our data but also by other censuses published in the annual breeding bird census issues of AUDUBON FIELD NOTES. In addition to the low general productivity of at least some southern pine forests, there is also a paucity of breeding bird species specifically adapted to the pine life form in the southeast. The abundant pine warbler (*Dendroica pinus*), the much less common brown-headed nuthatch (*Sitta pusilla*), and (on the Coastal Plain) the rather rare red-cockaded woodpecker (*Dendrocopos borealis*) are the only breeding species generally restricted to southern pines. All other birds in pine forests are either associated with the understory or with the tree life form in general. In fact, as can be seen from Table I, almost all of the birds of the two older pine forests also occur in the pure hardwood climax, with summer tanager (*Piranga rubra*) and possibly yellow-throated vireo (*Vireo flavifrons*) and crested flycatcher (*Myiarchus crinitus*) being slightly more numerous in the former. This situation is in marked contrast to that in the coniferous forest biome where numerous species are associated with and restricted to the conifer life form. In other words, there would seem to be a few vacant niches in southern pine forests, not only for specialized cone feeders such as crossbills, but for general foliage species as well. Before the coming of the white man, the geologically young, fire-maintained pine forests of the southeastern coastal plain were isolated from the northern forests (spruce, hemlock, white pine) of the mountains by the extensive hardwood forests of the Piedmont and lower mountain slopes. This might explain the paucity of specialized conifer birds breeding in the southeast. Following in the wake of clearing and cultivation, pine forests are now very extensive on the Piedmont and in the mountain valleys, so that northern and southern conifer communities are in closer contact. In this connection, the recent invasion from the mountains to the Piedmont by the blue-headed vireo (*Vireo solitarious*) is interesting and perhaps significant (see Odum 1948), since this species has nested exclusively in pine forests wherever it has appeared on the Piedmont (even though not so restricted in other parts of its range). This species first appeared as a breeder in the Athens region in 1948, a pair nesting on area 7 (but not in the year censused) and another nesting on pine area 8 in 1949. The black-throated green warbler (*Dendroica virens*) is another potential invader of southern pines (Odum 1950). Perhaps Nature is in the process of filling some of the pine forest niches!

As previously indicated, our study areas were relatively free from fire and other disturbances. In general, fire (as well as grazing) is not as important a factor in the Piedmont as in the Coastal Plain. As a result, Piedmont pine forests quickly develop a shrub and tree understory (previous field terracing also speeds up understory development), while Coastal Plain pine forests, especially long-leaf stands, may never develop a heavy understory due to fire and soil conditions. Thus, even very old or virgin forests remain open with the forest floor being covered with grass, herbs, and low shrubs. In such forests, grass-shrub birds such as Bachman's (pine-woods) sparrow (*Aimophila aestivalis*) and bob-white (*Colinus virginianus*) are characteristic.

The point to emphasize is that in pine forests of the southeast generally, it is the nature of the understory which largely determines the bird population. The breeding population of the pine overstory (composed largely of pine warblers) appears to show, at the present time, little variation with respect to geography or ecological age of the community.

The red-eyed vireo (*Vireo olivaceus*) and wood thrush (*Hylocichla mustelina*), which occurred in small numbers in the old pine forests (areas 8 and 9), and the cardinal were the three most abundant birds in the climax forest. It is interesting to note that in northern and middle eastern North America, where censuses have been made, the first two of these species are consistently among the top species in density in mature deciduous forests (Kendeigh 1944).

Comparison between breeding and winter populations.—Quay (1947) has investigated winter populations of various upland plant successional stages in the Piedmont of North Carolina. Since plant succession and winter avifauna are similar in North Carolina and Georgia Piedmont, it was deemed feasible to compare his results with those obtained in the present study. For his winter counts, Quay used a number of areas to obtain an average for different stages, since winter birds are much more mobile and larger samples are needed than is the case during the breeding season. In Figure 3, Quay's data are compared with ours, total density being indicated in birds per acre. Breeding density for all pine forests was lumped since Quay gives only one figure for pine forests in general. Likewise, winter data on grasslands were averaged.

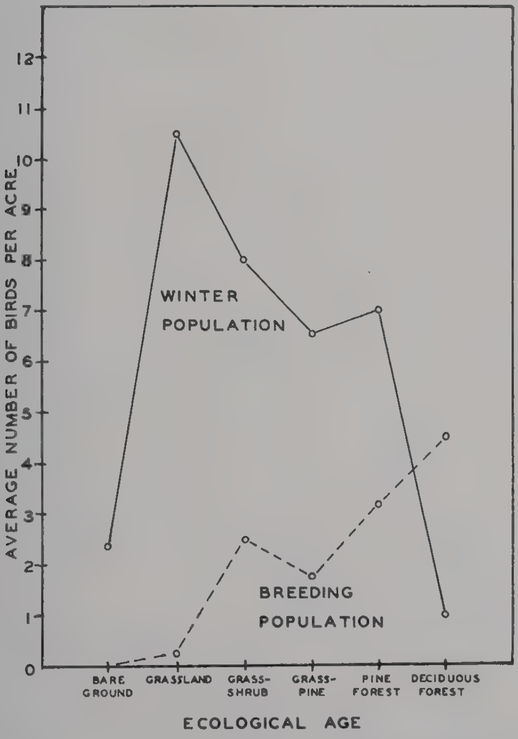

FIG. 3. Comparison of breeding and winter populations in the upland sere of Piedmont region of southeastern United States. Winter population data from Quay (1947).

The greatest density of birds was found in grasslands in winter, the crabgrass fields being especially attractive to large numbers of Savannah sparrows and meadowlarks. As can be seen from Figure 3, birds were much more numerous in the early stages of succession in winter than in summer, large numbers even frequenting "bare" fields. It should be pointed out that ground in these "bare" fields was never completely bare, there being some vegetation in the form of sprouting winter wheat or crabgrass patches. Thus, the bare ground stage is actually equivalent to a "0-year" or "1-year" stage in succession. Meadowlarks, killdeer, mourning doves, horned larks, pipits, starlings, etc. frequent this early stage in winter. Pastures were found to be similar to bare fields in winter populations. In general, the high density of grasslands in winter is due to large numbers of winter resident fringillids. Pine forests also showed higher populations in winter, the conifer-frequenting golden-crowned kinglet and other winter residents adding to the permanent resident populations. Only in the deciduous forest were the winter populations lower than during the breeding season. The cover, of course, is reduced in deciduous forests in winter, and 14 of the 23 species breeding in our oak-hickory study area (No. 10) migrate south for the winter.

Despite the fact that birds range more widely in winter, most of the common permanent resident species select about the same habitat in winter as in summer. The field sparrow, for example, proved to be the commonest bird in grass-shrublands ("old fields") both during the winter and summer. There is a general tendency, however, for many species (their numbers in some cases being augmented by migrants from further north) to shift to younger vegetation or to include a greater variety of stages within their winter home range. This is particularly true of species which require older vegetation for nesting, but find optimum feeding conditions in younger vegetation.

DISCUSSION

Forest edge species.—The reader will undoubtedly notice that many upland birds common in the Athens region (mockingbird and shrike, for example) are absent from the successional series as tabulated in Table I. These species require for their breeding territories two or more communities of *widely* different ecological ages (usually early and late stages of succession) intermixed, which explains their absence in samples of plant communities of relatively uniform ecological age. Such species have been designated as forest edge birds by many authors since they are often characteristic of the edge of a forest where grass and shrubs are available for feeding activities and trees for nesting or song perches. Verna Johnston (1947) demonstrated that the forest edge in central Illinois was a distinct community which had characteristic species not found in either the forest or the open communities.

The results of our study suggest a definite quantitative criterion which may be used to separate more precisely true forest edge species from other species living in the forest edge habitat simply because their requirements are satisfied by the forest or open communities alone. Any species known to be a common breeding upland bird of the region which does *not occur* or *occurs but sparingly* (as compared with their occurrence in the region as a whole) in plots of uniform habitat representing the major stages in succession, would qualify as a true forest edge bird. Thus, species *not* listed in Table I (excluding predatory and other wide-rainging birds and those with specialized nesting site requirements, such as swallows) but which are common upland breeders in the Athens area could be designated as upland forest edge species of the Athens region. Going through Burleigh's (1938) list of "The Birds of Athens" we find that the following species qualify according to this criterion: redheaded woodpecker, kingbird, mockingbird, robin, bluebird, loggerhead shrike, starling English sparrow, orchard oriole, chipping sparrow, and blue grosbeak. Also, there are a number of species which occurred but sparingly (less than 5 prs./100 acres) in the "pure-habitat type" plots (largely in transition communities) but which are common in the region. These species are: mourning dove, flicker, blue jay, catbird, brown thrasher, indigo bunting, and goldfinch. These species may be considered forest edge species of perhaps a somewhat less obligate class. Between 30 and 40% of common breeding birds of Athens region qualify as forest edge species.

This criterion of a forest edge species is based on the theory that, since a forest edge community is a mixture of early and late successional stages (grass and trees or grass, shrubs, and trees) and is best developed under the influence of edaphic conditions (soils or water differences), fire, or disturbance, a true forest edge will not develop during the course of normal or theoretical succession in a region where climate favors rapid development of the forest community. In such a succession, by the time the seedlings of tree species have developed into tree life form size, grass and shrubs will be greatly reduced or absent. In the succession on the Georgia Piedmont, pines often seed in so fast that even the shrubland is poorly developed, and there is no place for a robin or a mockingbird in the successional series. However, in actual practice the development of the forest is often irregular or retarded for one reason or another with the result that a well-developed forest edge community does develop on abandoned fields. For example, where several small cotton fields are abandoned gradually, large trees may have developed on the terraces while there is yet grass on the interterrace areas. In this case, of course, we really have two separate successions, one of which has been allowed to proceed much longer than the other, the combination of the two making the distinctive forest edge habitat to which a number of bird species are specifically adapted. In applying the above criterion of a forest edge species, care must be taken to select areas in which conditions are uniform. Once the true forest edge species have been determined, of course, the birds themselves may be used as excellent indicators of the nature of specific communities.

It is important to note that a species may be primarily a forest edge species in one part of its range and a forest or other "pure-habitat" species in another part of its range. For example, in the northern states the cardinal appears to be a forest edge species only (Johnston 1947). In the southeast, while it is common in forest edge habitats, it also occurs abundantly in the interior of natural forests, which, of course, disqualifies it from being a true forest edge species in this region according to our criterion. It may be that many forest species become primarily forest edge on the periphery of their range or in regions where forests have nearly all been destroyed. Ernst Mayr tells us (personal communication) that there are many more forest species which occur in towns and villages (a forest edge habitat) in parts of Europe than is the case in North America. He thinks studies of the bird populations of towns may show the beginning of such a trend in northeastern United States.

By way of conclusion, it should be emphasized that the ecology of complex or mixed communities can best be (perhaps can only be) understood after uniform or simplified communities in the successional series have been studied. Thus, even though uniform communities such as were selected in the present study may be uncommon or even rare under actual field conditions of the region, their importance in determining the factors which affect habitat selection and population density is very great.

Comparison with other studies.—In Europe and North America, a large volume of census work has been published, but in comparatively few instances have population changes within complete seres been worked out. As early as 1908, Adams discussed "bird succession" and listed characteristic species of successional stages from aquatic communities through bogs to climax forest on Isle Royale, Michigan. Although density was not measured, a greater variety of bird life occurred in the intermediate stages than in either the early or climax stages. One of the earliest and most complete quantitative studies of the relation of breeding birds to plant succession is that of Saunders (1936). He censused large acreages of various communities ranging from grassland to climax forest in the Allegheny State Park of southwestern New York, a region which lies in the ecotone between the eastern deciduous forest and the northern coniferous forest biome. Although the method used by Saunders, a strip count of singing males, is not the same as the territory-mapping method, the relative abundance and successional trends can safely be compared with those obtained in our study. In the upland sere, Saunders found that population density was low in grasslands (fields, 9 pairs per 100 acres), higher in shrublands (bushy pastures, 65), young forests (aspen-cherry, 127; aspen-red maple, 37), intermediate forests (maple-beech, 40; maple-beech-hemlock, 133), and highest in climax maple-beech-hemlock forests (182). Mature oak-hickory forests had larger populations than young or "sprout" oak-hickory. Lowland communities, such as meadows and stream-side forests, had a higher density than comparable stages on the upland. The highest density reported in the study was found in orchards, which are forest edge communities.

Kendeigh (1948) found a similar trend in his study of several successional stages in northern lower Michigan. Density was lowest in the grassland and highest in the mature forests. In another study of biotic communities of the deciduous-coniferous forest ecotone in eastern New York, Kendeigh (1946) found population density higher in a shrubland stage than in mature forests. However, the areas studied were abandoned fields with sizable trees (hedgerows) so that the "community of mixed shrubs and small trees" had considerable forest edge character and contained such breeding species as the red-eyed vireo and ovenbird as well as the yellowthroat and song sparrow. Such mixed communities represent several ecological ages, as previously discussed.

Odum (1950) studied breeding populations of three stages, *i.e.,* shrubland, intermediate forest, mature forest, of two seres, *i.e.,* oak-chestnut and hemlock, on the Highlands Plateau of North Carolina. In the drier communities of the oak-chestnut sere density was greater in the shrubland than in the forest. In the moist hemlock sere, density was also high in shrubland stage, but even higher in the climax hemlock-hardwood forest. It was pointed out that moisture was an important factor influencing bird density. Comparison with other studies in the Appalachian region indicated that mature coniferous-hardwood forests which develop a luxuriant understory in regions of high rainfall have higher bird densities (over 300 pairs per 100 acres) than either mixed forests in regions of less rainfall or climax forests of the Eastern Deciduous Forest Biome in general.

Very few comparisons can be made with the extensive British bird census work as reported in the *Journal of Animal Ecology* by Lack, Venables, Colquhoun, and others. Successional processes in the British Isles appear to be much altered by intensive and long-continued land use by man, open habitats being heavily grazed or forest edge in character and many of the forests being of the artificial or planted variety. Also, British workers have often used counts, rather than censuses, to determine habitat selection and relative abundance over large areas. Lack (1933), Lack and Venables (1939), and Venables (1939) found that there was a very definite succession of bird species accompanying habitat changes from grassland to afforested areas. Shrublands (or "scrub") had higher population density than grasslands, and deciduous thorn shrubland higher than coniferous shrubland in the "Downs" country (Venables 1939). Mixed broadleaved forests and natural pine forests had rich populations, but pine plantations were relatively poor in bird life (Lack and Venables 1939). Lack (1933) concluded that "birds are far more influenced by the height of the vegetation than by its nature" (p. 251).

Are there general conclusions or unifying principles which may be drawn from these scattered studies? It seems likely that in upland seres in forested regions where various stages (grassland, shrubland, etc.) remain in more or less pure form, and where there is sufficient moisture for complete development of the forest understory, an increase in bird population density (and probably number of species as well) may be expected to occur with increasing ecological age. Thus, as plants increase in height, volume, and diversity of life form, the available niches increase. This trend may prove to be basic where succession starts from "scratch," that is, from uniformly bare ground, and where edaphic factors (extreme water, soil or disturbance factors) are minimum in effect. Theoretically, the population density-succession curve should be a sigmoid one, as is characteristic of the growth of populations, with perhaps a downward trend as the mature forest community becomes overaged or senile. Data presented in this study and that of Saunders and Kendeigh seem, roughly at least, to fit this concept.

In hydroseres, where the water content of the habitat exerts a more direct effect, a density peak may be reached early in succession—in the marsh or shrub stage (Beecher 1942, Aldrich 1943)—even though a peak in number of species may occur later. Secondary seres which do not begin with bare ground (or water) such as succession which follows fire or logging appear to exhibit particular population patterns. Primary seres (priseres), in which succession is extremely slow with the early stages persisting for a long time, may show different populations changes from the rapid secondary seres. In other words, basically different types of seres in all probability exhibit basically different population patterns. At least, this possibility should be considered before wide-spread comparisons are made. In any event, simplified communities and seres should be sought out and studied in nature in order to bridge the gap between highly simplified, laboratory population studies on the one hand, and highly complex situations usually encountered in practical field work.

Possible effects of birds on plant succession.—It has often been assumed that birds and other animals are largely passive in plant succession, which would, therefore, proceed in the same manner whether animals were present or not. Theoretically, of course, this cannot be, since all organisms —plant, animal, and microorganism—are integral parts of the total community and ecosystem and have vital roles to play. In practice, there are well-documented cases where vertebrate animals have proven to be very influent or to actually control successional processes, as for example the well-known cases were deer alter plant succession by eliminating favored food plants and thereby allowing less palatable ones to become dominant. As far as birds are concerned, the picture is not clear and certainly needs more investigation. Probably birds have their more important direct effect on succession as the result of dispersion and/or destruction of seeds. For example, birds and small mammals have been shown to be very important in secondary succession following logging, slash burning or ground fires in long-leaf pine forests (Chapman 1938) and in Douglas fir or other western coniferous forests (Krauch 1936). When the ground is relatively exposed, the seeds of these conifers may be entirely consumed by animals before they have a chance to germinate. At the same time, birds bring in and "plant" cherries and other rapid-growing early seral plants with a resulting delay in the return of the climax (in the case of logging). This is recognized as a definite problem by foresters who, of course, desire to short-circuit or arrest natural succession as much as possible in order to speed the return of valuable timber.

On the southeastern Piedmont, the seeds of pioneer plants in old field succession are wind-dispersed for the most part, and it is not known whether birds play any part in their establishment. Keever (1950) has made a critical study of early stages of succession on abandoned fields. She was able to account for the horseweed-aster-broomsedge succession on the basis of the season of seed production, germination requirements, and competition. The time when the field was last cultivated during the summer was found to be important and seeds of pioneer plants were found in the soil after cultivation ceased. No mention was made of possible animal influence. Since large numbers of birds are found in winter in fields last cultivated the preceding summer ("bare ground" and crabgrass stages, Figure 3), there is a possibility that birds may be important agents of seed dispersal and/or seed destruction. Pine seeds reach abandoned fields usually as the result of wind, and since broomsedge provides thick cover, seeds are not likely to be removed in large numbers by animals, as sometimes occurs in the post-logging succession mentioned above.

In contrast to the pioneer grasses, forbs, and pines, many species of woody plants of the shrublands (blackberry, sumac, cherry, and hawthorn) and many of the important understory and dominant trees of later stages (persimmon, dogwood, and oaks) have fleshy or dry fruits which are eaten and whose seeds are distributed by animals. We have noticed that where fields adjoin forest edges and floodplains (habitats rich in birds and fruit-bearing plants), a shrubland develops to a much greater extent than where fields are surrounded by young pinelands. In the latter case, pine often succeeds broomsedge directly, completely skipping a shrubland. As already indicated, terraces are very important on the Piedmont. The presence of sumac and persimmon on these terraces often long distances from any possible seed source can only be ascribed to activities of animals. A well terraced abandoned field thus invariably develops a shrubland stage and many of the plants have such a head start that they are never shaded out by pines and thus become pioneer elements of the climax forest. Referring back to the list of important plants found in the study areas of grass-shrublands and young pine forests, we find that all but two of the deciduous woody species must depend on animals, perhaps birds, for establishment at any great distance from the seed source. Once the climax forest is established, it is probable that birds are less important in this respect since a seed source for reproduction of climax plants is close at hand.

To summarize, on the southeastern Piedmont, birds (and mammals) probably have their most important influence during the intermediate stages of succession, at which time a large percentage of dominant plants may be animal-dispersed. During the transition between grassland and forest, birds are especially important in determining to what extent a shrubland stage will develop.

SUMMARY

1. Ten 20-acre areas representing successive stages in the secondary upland sere of the Piedmont region of Georgia, and three areas of cultivated grassland were censused for breeding birds using the territory-mapping method. Essentially, the series of seral stages involved four broad plant life forms which succeed one another as follows: grassland (grass and forb dominants), shrubland, pine forest, and hardwood forest (oak-hickory) (Fig. 1).

2. Breeding bird densities of 15 to 40 pairs per 100 acres in recently abandoned fields increased to 136 in 20-year-old shrublands, decreased to 87-93 in young pine forests, and increased as the hardwood understory developed in older pine forests to 239 pairs in a 100-year-old pine stand and 228 in a young oak-hickory stand (Table I). Thus, a trend toward increased density (and also number of species) with succession from bare ground to the late sub-climax or young climax was interrupted by low densities encountered in young pine forests (Fig. 2).

3. Most species had a very definite range of occurrence in the sere but a few, notably the cardinal, persisted through many stages.

4. There were only two species of true grassland birds, the grasshopper sparrow and meadowlark, but a third species, the horned lark has recently invaded the region. Cultivated grasslands (pastures, etc.) had the same two-species population as 1-3 year abandoned crop fields (Table II), but ground cover was thicker and bird populations denser in the cultivated areas.

5. Several possible reasons for low density in pine forests were discussed, and the recent invasion of the blue-headed vireo into this habitat was noted. Species composition and density in pinelands depends largely on the nature of the understory, the pine warbler being the only very common species strictly associated with the overstory, or the pine life form in general.

6. Density and composition of bird population of the oak-hickory climax resembled that of other deciduous forests of the eastern United States.

7. Comparison of breeding population with Quay's (1947) data on winter population of similar seral stages (Fig. 3) revealed that early stages had a much higher bird density in winter, due especially to the large number of winter resident fringillids. Birds were also more abundant in pine forests in winter, and only in hardwood forests were summer densities higher.

8. The results of the study of "uniform-aged" habitats suggests a clear-cut quantitative criterion for defining true forest-edge birds (that is, species which require for their breeding territories a combination of two or more communities of widely different ecological age, usually early and late stages in succession), as follows: species which are absent or uncommon (less than 5 pairs per 100 acres) in a series of even-aged stands representing major stages in the sere, yet which are common in the region as a whole are true forest-edge species. According to this criterion, about 30 to 40% of the common breeding species of the region are forest edge in their habitat requirements at the present time.

9. Birds appear to exert their greatest effect on succession during the intermediate stages, especially during the shrub stage and during the invasion of hardwoods.

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YEARLY SOIL TEMPERATURES IN EASTERN NORTH DAKOTA[1]

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INTRODUCTION

Soil temperatures, and particularly soil frost, is a topic, like the weather, of which many people are aware but few know much about. Studies of the yearly cycle of soil temperatures are rare. In northern areas, extreme winter conditions not only make field work inconvenient, but also present instrumentation difficulties. Some studies relate to a short period of soil frost, maximum soil temperature, or comparative effects of cover types. It was the purpose of this study to obtain records of the changes in soil temperature throughout the entire year. To obtain this basic information, important to a variety of problems, series of thermocouples were established at depths of one inch to 6 feet at 5 different sites on the North Dakota Agricultural College campus at Fargo, North Dakota, and weekly readings were obtained for a two-year period from July, 1952, to August, 1954.

In the northern Great Plains, a critical period for woody perennial plant growth is the winter season when frozen soil makes water unavailable and cold temperatures increase water viscosity, while at the same time reducing conduction, respiration, absorption and root growth. During this time, winter desiccation, called parch blight, frequently occurs. The depth to which soils freeze where tree growth such as orchards or shelterbelts are involved may be an important factor in their survival. The reduction in wind velocity in these areas with the resulting accumulation of snow is an important consideration.

In this region there is a general tendency to seed small grains as early as possible. This is intended to make the fullest use of soil moisture of the spring and early summer rainfall, to avoid the summer drought, and in many cases to reduce the intensity of plant diseases. Excessive soil moisture and soils that are frozen or too cold for plant growth inhibit early planting. Records of the seasonal changes in soil temperatures should provide fundamental information to correlate with root development of crop plants.

Because snow usually accumulates throughout the winter with a major period of melting occurring in early spring, the receptivity of the soil to water infiltration at that period becomes a critical factor in storing the moisture from the long winter period. The run-off from frozen ground results in loss of soil moisture and in flood conditions. Where the drifting snow can be stopped on the field it reduces the frost depth, increases the infiltration of meltwater and reduces flooding and is thus manifold in its advantages, Matthews (1940). This additional moisture has been a major factor in the success of the shelterbelt program in the northern Great Plains, Stoeckler and Dortignac (1941). Spaeth and Diebold (1938) have reported a detailed study of the interrelationships between soil characteristics, water tables, temperature, snow cover, vegetation, and flood control from forest, pasture, and field in south-central New York.

With the northward extension of the use of corn, there is need for more information concerning the rate of warming of cropland in the spring and summer. Where the growing season is barely sufficient for corn to mature, it is essential to plant the crop as quickly as soil temperatures will permit in the spring. Weaver (1926) reports the minimum temperature for germination of corn to be 49°F. in contrast to wheat at 40°F., while the optimum is 93°F. in contrast to 84°F. for wheat.

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[1] Paper No. 9, Journal Series, from the North Dakota Institute for Regional Studies.

METHODS

Two of the 5 sites selected for the study were to compare the effects of snow depth as represented by corn cropland in open fields versus corn land where deep winter snows accumulated behind a shelterbelt (Site A vs. Site B). Because of changes in Experiment Station plans, however, both sites were in weedy, disced fallow after the first season. The third site (C) was in an adjacent apple orchard where wheat was planted in July or August and grown as a mulch crop between the trees. The fourth site (D) was maintained in a good lawn sod of Kentucky bluegrass which was frequently mowed. The thermocouples were located near the center of a large lawn to avoid the accumulation of snow in the form of drifts, thus being comparable in exposure to open field conditions. The fifth site (E) was in small grain stubble under open field conditions from one fall to the next and was fall plowed the second year. The history of these sites is summarized in Table I.

TABLE I. Field treatment of soil temperature sites

Dates	Sites				
	A	B	C	D	E
Aug. 1952....	corn	corn	wheat mulch	grass sod	....
Oct. 1952....	stubble	stubble	....	....	grain stubble
July 1953....	plowed	plowed	plowed	....	mowed stubble
Aug. 1953....	....	....	wheat planted for mulch	....	....
Oct. 1953....	....	....	....	....	plowed
June 1954..	....	....	plowed	..	....
Oct. 1954....	fallow	fallow	fallow	....	fallow

Except for Site B, which was located near the south side of a dense hedgerow of *Caragana* shrubs where snowdrifts reached a maximum depth of 10 feet, all sites were equally exposed and the differences in depth of snow were principally a result of the effectiveness of plowing, grass, stubble, or mulch cover to stop snow.

The thermocouples used in this experiment were made of #18 iron and constantan wires. About 1¼ inch lengths of bare wire were tightly twisted together in ten complete turns. The thermocouples were then waterproofed with two coatings of cellulose acetate and wrapped with rubber tape. Protection from weathering and damage by rodents was provided the wires leading from the thermocouples to the potentiometer. The wires for the eight levels of testing were pulled through a rubber tubing leaving each thermocouple and several inches of wire extending out through a hole in the tubing at the proper level. This short piece of wire and the opening in the tubing were waterproofed with rubber tape.

Thermocouples were placed at depths of 1 and 6 inches and at 1, 2, 3, 4, 5, and 6 feet. Those at the 3 lower depths were lowered into a soil auger hole and the hole carefully backfilled, using the dirt removed, with slight packing around each thermocouple. The upper 5 thermocouples were inserted into the sides of a hole made by a post-hole auger and the hole filled with the soil of the appropriate level. Previous experience using a series of thermometers inside a closed pipe inserted into the ground had shown that the temperature at different soil levels could be measured regardless of amount of pore space, so that the actual amount of compaction of soil around the thermocouples was not believed to be critical, except as it would affect soil moisture content and this, in turn, soil temperature.

The lead wires were run horizontally for several feet, just below the ground level, then up a permanent post and connected to a row of eight, male phone jacks mounted in a board at the side of a small platform used to hold the potentiometer.

The instrument used to determine soil temperatures was a Brown Portable Potentiometer, Model 1117, which is capable of measuring units of .01 millivolts or 0.35°F. To protect the wet cell of the potentiometer from freezing, a box was constructed around three sides of the potentiometer and insulated with vermiculite. A cold junction of 32°F. was provided by an attached thermos bottle which was filled with cracked ice and water into which was inserted an iron-constantan thermocouple. Connections were made to each thermocouple by means of a female phone jack with lead wires attached to the cold junction thermocouple and to the potentiometer. Readings taken in millivolts were later transcribed to tables and graphs as °F. temperature.

Measurements were taken weekly throughout the entire year. The readings were usually taken at 11:00 A.M. In addition to the temperature of the 8 soil depths, measurements were recorded of snow depth and air temperature. The average weekly air temperature which is included in the report was obtained by averaging the daily mean temperatures for each weekly period as they were reported by the U. S. Weather Bureau Station at

Hector Airport in Fargo, which is within a mile from the soil temperature sites.

Results and Discussion

Because the results of this study are based on a relatively short period of observation in contrast to the basis of average meteorological phenomena, which can only be presented as averages after several decades of observations, the results in this report indicate the effect of vegetative cover, cultural practices, depth of snow, etc. on soil temperatures for the period of 1952-54.

Effect of crop practices and vegetative cover

The best comparison of the effect of cultural practices and cover on summer and winter temperatures can be made for the year 1952-53 from these sites in open field conditions. These would be A (corn and stubble), C (wheat mulch), D (grass sod), and E (small grain stubble for winter data only).

Heat penetration and loss.—The effect of vegetation in shading the soil and thus preventing the absorption of solar radiation was particularly noticeable only in the corn plot of 1952-53, Table II. Here the heating of the soil, as indicated by the date of maximum temperature at the 6-foot level, was delayed for 1½-2 months after that of open fields of light mulch or grass sod.

Table II. Dates of maximum and minimum temperatures at the 6-foot depth

	Sites			
	A corn stubble fallow	C wheat mulch	D grass sod	E grain stubble fallow
Date of 1952-53	Oct. 24	Sept. 5	Aug. 16	....
max. temp. 1953-54	Oct. 3	Oct. 3	Oct. 13	Oct. 24
Date of 1952-53	Apr. 11	Feb. 14	Feb. 14	Mar. 20
min. temp. 1953-54	Apr. 3	Apr. 3	Apr. 3	Apr. 3

The delay in heat penetration under a corn crop during the summer was reflected in approximately the same lag (about 8 weeks) in the date of minimum temperature at the 6-foot level. Although important in affecting the time of minimum temperature, it did not affect the actual minimum temperature attained as compared to other sites.

In the following July (1953), the corn stubble was plowed. Under the fallow condition with full exposure of the black soil to insolation, the time lag in heat penetration was lost and the 1953 data show a date of maximum heat penetration similar to that of the other open-field sites.

From the data over a two year period, there is little or no apparent effect of clipped grass cover in delaying the heat penetration of the soil to a 6-foot level in comparison to fallow land on which grass and broad-leaved weeds reached heights of 4 to 6 inches before being disced or plowed.

Maximum temperatures.—The significance of vegetation in reducing the maximum temperature reached at each level is slight, as indicated in Table III. A comparison of the maximum temperatures at various levels for 1952-53 shows those of grass sod to be consistently below those of fallow land or wheat mulch except at the one-inch depth of the latter which may be due to a local difference more effective at surface levels.

Table III. Maximum-minimum temperatures at each level (1952-53)

	Sites			
Depth	A corn stubble fallow max.—min.	C (wheat mulch) max.—min.	D (grass sod) max.—min.	E (stubble-fallow) max.—min.
1 in.	82 — 23	76 — 25	81 — 26	 21
6 in.	74 — 25	74 — 26	71 — 29	 23
1 ft.	72 — 28	72 — 28	67 — 30	 25
2 ft.	66 — 30	67 — 29	64 — 32	 29
3 ft.	62 — 32	64 — 33	62 — 32	 31
4 ft.	62 — 33	62 — 35	61 — 34	 33
5 ft.	59 — 35	60 — 36	59 — 37	 34
6 ft.	58 — 36	58 — 38	57 — 38	 35

Minimum temperatures.—In regard to minimum temperatures at the various levels, the effect of grass sod was most evident. With the exception of the site under deep snow (Site B), the temperatures to which soils under grass sod were reduced were generally somewhat higher than sites under other cultural practices. Examination of the curves which were constructed also indicates that the site of grass sod exhibited the least fluctuations in temperature from week to week. Considering the dense mat of fine living roots in addition to a high humus content, this might be expected. The insulating value, or low thermal conductivity of organic matter is well-recognized and especially of dry organic matter, *e.g.*, dry peat has a thermal conductivity of about ⅛ that of wet peat (Benninghoff 1952). As mentioned earlier, records were not available on soil moisture so no evaluation of differences due to changes in specific heat or heat conductivity can be made.

The effect of litter in reducing frost depth is not as evident in this experiment as is reported from areas of shorter and less intense periods of cold. Goodell (1939) reports frost depths in Illinois of 5.5 inches for cornfields vs. 0 inches in adjacent woods. Scholz (1938) reported frost penetration of 10 inches in pasture and 4 inches in woods in Wisconsin with similar snow cover. Atkinson and Bay (1947) reported bare plowed soil as freezing to depths 2½ times that of pasture soil and 5 times that of hardwood woodlots. One of the most detailed studies is that of Kienholz (1940) in Connecticut reporting site variations of maximum frost depth of 8.5 inches in plowing, 5.9 inches in light sod, 5.0 inches in heavy sod, 3.9 inches in mixed hardwood, and 2.9 inches in white pine forest. In comparing forest soils with normal litter to soils denuded of litter, MacKinney (1929) found reductions of 60-80% in diurnal temperature fluctuations. The presence of litter also delayed autumn freezing and spring thawing and reduced the depth of freezing.

It will be pointed out later, however, that where vegetation affects snow depth as within or to the lee of shelterbelts, that marked differences occur in frost penetration.

Frost duration.—The length of time that frost was present at each level of the several sites is given in Table IV. Because the surface layers are first to freeze and usually first to thaw, the total period of presence of frost in the ground may often exceed the frost duration at any one level. Obviously freezing always proceeded from the surface and downward to its maximum depth. This was not always true of thawing, however.

TABLE IV. Number of weeks frost was present at various levels (average of 2 years readings)

Depth	Sites			
	A (stubble-fallow)	C (mulch)	D (sod)	E (stubble-fallow)
1 in.	19.5	17.5	11.5	17
6 in.	15	12	15	16
1 ft.	12	11	7	13
2 ft.	8	4	0.5*	11
3 ft.	....	....	0.5*	2.5
4 ft.	....	....	....	....
5 ft.	....	....	....	....
6 ft.	....	....	....	....
Frost-free period (wks.):	32	34.5	36.5	33

*Due to a questionable low reading of one date, possibly due to unbalance of standardizing cell.

Thawing.—Reports of thawing have been variable as to the progression of the temperature increases. It is generally considered that thawing starts at the surface and proceeds downward, yet, the common expression, "the frost comes 'out' of the ground" literally expresses the opposite concept. Examination of the temperature curves from the 4 open field sites for two springs show that both ideas are correct. Where the soil had frozen to the 3-foot depth and was subsequently subjected to a period of 2 to 3 weeks of thawing, surface temperatures increased most rapidly and thawing progressed downward to a foot depth. Meanwhile, with the lack of additional cooling from above, thus reducing heat loss upward, the frozen layer received heat by conductivity from the unfrozen soil below. Thus, the 3-foot level thawed out before the 2-foot level, while the temperatures of lower levels were also increasing. The last measured level to thaw was either the 1- or 2-foot level. This is very similar to the thawing pattern described by Scholz (1938) in an open pasture in Wisconsin and by Kienholz (1940) in Connecticut soils which were plowed, grass sod, or forested. Both authors found the last frost to be about halfway between the surface and the maximum frost depth.

Frost-free period.—Reference again to Table IV shows the net effect of grass cover, leaf litter, and high humus content. The soils under sod (Site D) are nearly consistent in having all levels frozen for the minimum time when compared to the levels of other sites. Furthermore, the total frost-free period, which represents the time from the last spring ground frost to the first fall frost, exceeds all other sites by much as 4½ weeks. This is principally due to the lack of wide soil temperature fluctuations under grass sod and particularly to the delayed first freezing in the fall of 1953 which was as much as 7 weeks after that of plowed fields (A and E) and that of thin wheat mulch (C).

One other aspect of soil temperature affected by vegetative cover is the spring date at which the entire soil is free of frost. This does not mean the date at which the soil can be worked, but it is significant in the receptivity or infiltration capacity of the soil for snow melt, flood waters, or early spring rains. Here again, the stability resulting from the insulating effect of the grass sod was important in preventing re-occurring spring frosts of the surface layers. As a consequence, the site in grass sod was frost-free 4-8 weeks earlier than the other sites of comparable snow depth in 1952-53 and 2-4 weeks earlier in 1953-54.

Effect of snow depth

Many studies which have been reported on soil temperatures, particularly minimum temperatures, have been from forested northern states where winter snows are common. In studies comparing sites of different vegetative or litter cover, the comparisons often become confused by varying depths of accumulation of snow. Snow, with its myriads of air spaces, acts as an excellent insulating layer decreasing the heat loss from the soil.

To determine the effect of deep snow cover in contrast to normal open field conditions, Site B was established near the edge of the same field in which Site A was located and adjacent to the south side of a tall, dense, *Caragana* windbreak. During the previous year, snow had accumulated over the area in a drift about 9 feet in depth. Cultural practices, slope, and exposure during the summer were the same for Sites A and B.

Time, duration, and depth of snow.—Both sites received snow at the same time, of course. During 1952-53 snow was on the ground for 16 weeks at both sites and in 1953-54 for 18 and 19 weeks at Sites A and B, respectively. In 1952-53, the maximum snow depths were 4.5 in. and 36 in. at A and B; in 1953-54 the maximum depths were 9 in. and 120 in.

Temperature effects of snow cover.—Prior to the rapid accumulation of snow, which in 1952-53 increased to 3 feet in a period of one week, the soil temperature curves were similar. At the time of the beginning of snow accumulation in 1952-53 only the surface layers of 1 in. to 1 ft. were frozen. In the open field, the temperature continued to decrease at all levels until the frost depth reached 3 feet and the 1 in. layer was as much as 9°F. below freezing. During the same period, the deeply snow-covered site showed a marked leveling off of temperatures at all depths. Frost had previously penetrated to the one-foot depth and the 1 in. layer was 4°F. below freezing. With the snow cover, the temperatures of the 1 in., 6 in., and 1 ft. levels adjusted to approximately 32°F. The general soil temperatures were about 5°F. higher than in the open field site at the time in March when the soils began to warm up.

The effects of snow cover were even more outstanding in 1953-54. Soil temperatures were similar prior to a three-week period when drifting piled snow over the site to a depth of 10 feet. During the following 5 weeks, the soil temperatures actually showed an increase in temperature at all levels with a removal of frost from the surface layer. Not only did the frost leave the 1 in. level but the temperature rose to several degrees above freezing. During the same period of time, the general soil temperatures of the open field including the 6-foot level, dropped about 10°F. and frost penetrated to the 2-foot level. As the snow melted, there was a cooling of all levels in site B and the minimum temperatures were reached at the end of March when the snow cover had decreased to a depth of only 18 inches.

In a study of snow drifts in North Dakota shelterbelts in 1952, the writer observed that the ground was entirely free of frost where the belt was covered with snow to depths exceeding 3 or 4 feet (Potter 1952). It was assumed that the litter and duff within the belt served to delay freezing until the snowfall provided an insulating cover. A second possibility was also suggested, that if frost had previously occurred, the insulating effect of the snow cover might have allowed the soil to have thawed out from below due to the retention of residual heat in the soil. The latter assumption has now been demonstrated to be possible. This effect of snow cover in preventing the formation of soil frost or in thawing it from below is extremely important in the effective infiltration of snow melt which would otherwise be run-off from frozen ground (Stoeckeler and Dortignac 1941). The reduction in soil frost is also important to woody perennials throughout the winter season in making available the soil water from the unfrozen soil, thus decreasing the danger of winter desiccation or "parch blight."

In Table V are given the average minimal temperatures at the two sites. The effect of the snow is, of course, most obvious in the surface layers, but the 3-4°F. difference in the deepest layers is most revealing of the real insulating effect of the snow.

TABLE V. Minimum temperatures (°F.) at each level (average of two years)

Depth	Site A (open field)	Site B (deep snow)
1 in.	22	29.5
6 in.	25.5	31
1 ft.	28	32
2 ft.	30.5	33
3 ft.	32	34
4 ft.	33.5	35
5 ft.	34.5	37
6 ft.	35.5	39

Table VI indicates the periods of time from the first frost to the last frost at each level. Although there are definite differences in the two sites, the real picture is not revealed, since the freezing temperatures in the site under snow occurred before and after the drift accumulation. For example, in 1953-54 the 1 in. depth was actually frozen at 6 different weekly readings. The total period from first to last frost at the 1 in. depth was 18 and 16 weeks for Sites A and B. However, the actual weeks when the soil was frozen at that depth were 15 and 6, respectively. The 6 in. and 1 ft. depths once frozen remained frozen in the open field and in the site under snow were not frozen until after much of the snow had melted away.

Table VI. Weeks from first to last frost at each level (average of two years)

Depth	Site A (Open Field)			Site B (Deep Snow)		
	1952–53	1953–54	Aver.	1952–53	1953–54	Aver.
1 in.	21	18	19.5	12	16	14
6 in.	13	17	15	11	1	6
1 ft.	10	14	12	7	1	4
2 ft.	5	11	8	...	...	...
3 ft.	1	1	1	...	...	...
4 ft.	...	...	...	...	...	...
Entirely frost-free.	31	33	32	40	36	38

Spring and fall temperature overturn

Thermal overturn is a term long used in limnology referring to a period of time when all the levels in a body of water reach essentially the same temperature and density. This occurs at 39°F. Following this condition in the fall, water decreases in density as temperatures drop below 39°F. and the lighter, colder water remains on top where it may solidify into ice. As the ice melts in the spring and the upper layers of cold water are warmed to 39°F., they tend to settle resulting in a mixing at a rather uniform temperature throughout of 39°F. This is the period of spring overturn. Subsequently as the temperature of the surface layers rises above 39°F., they decrease in density and a lighter, warmer stratum develops near the surface and continues to deepen during the summer. In the fall, the reverse process occurs.

In soils there is no actual mixing as in water, but there is a similarity of having the lower levels warmer in the winter, a short period of rather uniform temperature throughout, and then warmer upper levels in the summer. On examination of the temperature curves for the 5 sites and the two-year period, the writer was greatly surprised to find a distinct, brief period in the spring and fall when the temperature lines converged, coincident with the reversal of the order of temperature gradient. Although the uniformity of temperature is not so exact as in lakes, due to lack of mixing currents, it is a definite phenomenon of great similarity and is herein referred to as the spring and fall soil temperature overturn.

The dates and temperature variations at each level from 6 inches to 6 feet during the fall and spring overturns are given in Table VII. Temperatures from the one-inch depth have been excluded because they are so erratic and in short periods of time are affected by local conditions such as clouds, etc. The time and temperature ranges are surprisingly uniform. When the results of the 5 sites and two years are averaged together, the average fall overturn date is October 3 with an average temperature variation between depths of 2.4°F., from 57.1-59.5°F. The average spring overturn date is May 5 with an average variation of 2.1°F., from 39.9–42.0°F.

Table VII. Dates and temperature ranges of fall and spring overturn (6 in.-6 ft.) in °F.

Site	Fall			Spring		
	1952-53	1953-54	Aver.	1952-53	1953-54	Aver.
A	55-58 Oct. 3	58-61 Oct. 17	56.5-59.5 Oct. 10	38-40 May 2	39-40 May 9	38.5-40 May 6
B	56-60 Sept. 26	60-62 Oct. 3	58-61 Sept. 30	48-49 May 2	41-43 May 9	44.5-46 May 6
C	56-60 Oct. 3	60-61 Oct. 3	58-60.5 Oct. 3	41-44 May 2	40-41 May 9	40.5-42.5 May 6
D	54-56 Sept. 26	60-61 Oct. 3	57-58.5 Sept. 30	41-44 May 2	40-41 May 9	40.5-42.5 May 6
E	......	56-58 Oct. 3	56-58* Oct. 3*	36-41 May 2	35-37 May 1	35.5-39 May 2
Aver.	......	......	57.1-59.5 Oct. 3	......	......	39.9-42.0 May 5

*One year only.

These dates of overturn indicate a 5-month period during which the soil is progressively cooler with increasing depth and a 7-month period with an inverted temperature gradient.

Mean annual temperatures at each depth

One of the interesting features of the study was the remarkable uniformity of the yearly mean temperatures at all levels at each site. The mean annual temperatures given in Table VIII are the averages of the weekly readings over a two-year period for each level. It should be noted that due to the insulating effect of deep snow for an extended period of time, the annual mean temperatures of Site B are about 3°F. higher at most levels than those in an adjacent open field with little snow, Site A. Also, the yearly mean temperatures of the soil under grass sod, Site D, are about 1.5°F. higher than those of Site A. The mean yearly temperatures under grass sod are most uniform with a variation of only 0.6°F. in comparing the 8 levels from one inch to 6 feet.

Yearly temperature curves for open field

As an example of the yearly temperature curves, one site and several depths were selected for illustration from the two-year study of 5 sites. In Fig. 1 are shown the results from the 1953-54 data of Site E which was plowed in October, remained as plowed and fallow throughout the rest of the

Table VIII. Yearly mean temperature (°F.) for two year period

Depth	Sites		
	A (open field, little snow)	B (deep snow)	D (grass sod)
1 in.	47.7	54.8	48.5
3 in.	46.7	48.6*	48.1
1 ft.	46.7*	50.3	48.5
2 ft.	47.0	50.0	48.4
3 ft.	47.0	49.9	48.5
4 ft.	47.0	50.3	48.6
5 ft.	47.0	50.2	48.7
6 ft.	46.9	50.1	48.6

*One year only.

period, and was not in an area of snow accumulation. The curve for air temperature represents the weekly average for the mean daily temperatures of the 7 days prior to each reading. These were obtained from the U. S. Weather Bureau Station which is less than a mile from the sites.

In many instances, the effect of the weekly air temperature is best revealed at the levels observed near the surface. Exceptions occur where the surface layers are affected at the time of reading by temperatures which may not correspond to the weekly mean. The time lag in response to the cold period progressively increases with increasing depth. At the 6-foot level, the time lag after the period of minimum air temperature amounts to about two months.

Attention is directed to the short period of several weeks between the frost-free period and the spring overturn in temperature, at which time the temperature gradient reverses. The prevailing temperature at this time is close to the minimum for the 6-foot level. So to, the time and temperature of the fall overturn nearly coincide with the time and degree of maximum temperatures of the 6-foot level.

It is difficult to ascribe a minimum temperature threshold for the physiological activity of microorganisms, even more so for higher plants, but of course the rates of chemical activity decreases greatly approaching freezing temperatures. To point out the period of time when the soil levels were below freezing, a line has been included at the 32°F. level. Surface soils were frozen for over 18 weeks and frost penetrated to the 3-foot depth for over two weeks. The temperature of 40°F. has often been used as a temperature threshold. Note the long period of time that most of the soil is below this temperature.

Small grains are often planted at a time corresponding closely to the spring overturn with a soil temperature of about 40°F. On the College Experiment Station plots, hard spring wheat was first planted on April 23, 1953, April 14, 1954, and on the average on April 19. This time of first planting occurs about two weeks prior to the spring overturn. Soil temperatures at this time are nearly minimum for germination and root growth would proceed slowly and penetration of vertical roots would be limited by the rate of warming of surface soils. The only root habit studies available for hard spring wheat in this region are the early studies of Ten Eyck (1899) which did not trace the development of the root system through the season but reported extensive roots throughout the top 4 feet and some roots to 6 feet. Weaver (1926) reported the development of spring wheat roots in eastern Nebraska from a planting date of April 1. The working level at several ages were: 6.5 inches in 30 days; 10 inches in 45 days; 18 inches in 60 days; and 36 inches in about 90 days. To illustrate the inhibitive effect of cold soil, the root system of 25-day old plants which were planted May 5 exceeded those of 45-day old plants planted April 1.

Following a uniform temperature of about 40°F. at planting time, there is a progressive increase in temperature from the surface downward, which is apparently accompanied by increasing depth of root penetration as temperatures approach the general optimum for root growth of 65-70°F. At the time of maturity of wheat, the soil temperatures within the working level of the roots (the upper 4 feet) ranged from 55-65°F. Only the surface foot reached the optimum temperature of 65°F. by the end of the root growth period the last of July and roots in the 5-6 foot zone were at temperatures of about 50°F. It would appear therefore, that wheat roots are developing at a temperature disadvantage throughout the season in the heavy clay soil at Fargo.

Because the minimum temperatures for germination and root growth are higher for corn than for wheat, corn planting is delayed until June. The root studies of corn by Ten Eyck (1899) show that corn planted June 11 produced roots which in a month's time were principally of lateral development with most roots in the upper 8 in. of soil. From the writer's present study, soil temperatures at 6 to 12 inches during this time would be slightly over 60°F. Ten Eyck also observed that by August 4, many of the adventitious roots developing from upper nodes penetrated the soil more deeply than earlier roots, reaching depths of 2.5 feet and that the downward growth was more rapid when the soil was relatively dry. The dryness would result in the soil being relatively warmer. Again from the present study, soil tem-

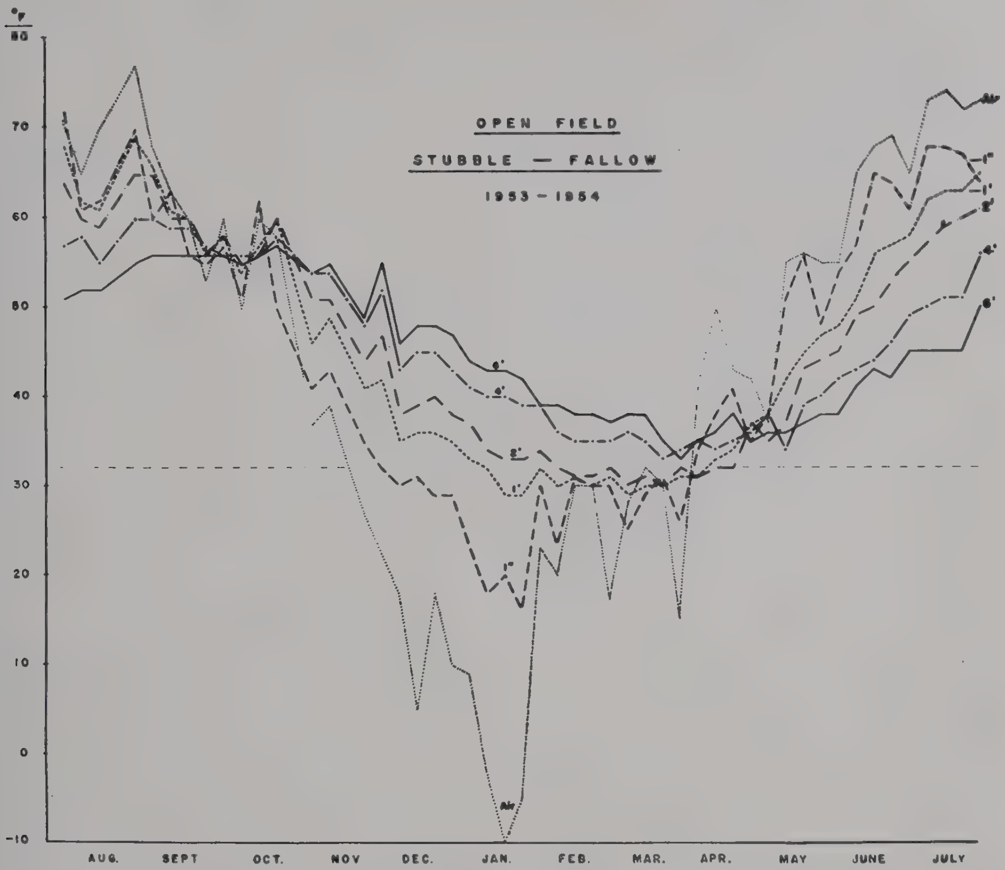

Fig. 1. Soil temperatures (Site E, 1953-54) under open field conditions of small grain stubble until plowing in October. Maximum snow depth of 9 inches, common to open field plowing. Temperatures at 6 in., 3 ft., and 5 ft. omitted from the graph.

peratures on August 4 at the 2.5 foot level would be 60-65°F. From August 4 to September 18, Ten Eyck reported well-developed root growth extending downward to 3.5 feet. During this period, the temperatures of this level would have reached 60-65°F., as indicated by the present study.

Summary

Soil temperatures at depths of 1 and 6 inches and at 1, 2, 3, 4, 5, and 6 feet were determined at 5 different sites, varying in cultural practice and snow cover, at Fargo, North Dakota from July, 1952, to August, 1954. These were based on potentiometer readings of iron-constantan thermocouples.

The greatest lag of heat penetration into the soil and of heat loss from the soil, as evidenced by the dates of the maximum and minimum temperatures at 6 feet, was observed under a corn crop. These temperatures were reached 1½-2 months after those of plowed fields, wheat mulch, and grass sod.

Field crops or grass sod had a slight effect in reducing the maximum temperatures reached at each soil depth. The insulating effect of grass sod resulted in higher minimum temperatures than under stubble or fallow land.

Thawing was observed to occur both from below and above with the last level to thaw being somewhat intermediate between top and bottom of the originally frozen soil.

The total frost-free period under grass sod was as much as 4½ weeks longer than that of plowed fields or of wheat cover used as a mulch in an orchard.

Comparisons of soil temperatures were made between open field conditions and soil conditions under deep snowdrifts behind a shelterbelt. The accumulation of snow resulted in the thawing out

of frozen surface layers and the maintenance of soil temperatures several degrees warmer than in adjacent open fields.

In fall and in spring, the soil reaches a uniform temperature throughout, comparable to the spring and fall overturn in lakes. The average spring overturn of soil temperature was on May 5 with an average variation of 2.1°F. from 39.9-42.0°F. The average fall overturn was on October 3 with an average temperature variation of 2.4°F. from 57.1-59.5°F. These results include soil levels from 6 inches to 6 feet. The time and the temperatures of the spring and fall overturn correspond closely to the time and temperature of the 6-foot level when at the minimum and maximum temperatures, respectively.

The mean annual temperatures of the various levels from one inch to 6 feet were remarkably uniform at each site. Due to the insulating effect of winter snow in a deep drift, the mean annual temperatures for that site were about 3°F. higher than in an adjacent open field. The temperatures under grass sod were about 1.5°F. warmer than in plowed fields and were the most uniform with a variation of only 0.6F. for the mean annual temperatures of the levels between one inch and 6 feet.

Yearly temperature curves to the 6-foot depth are given from an open field site of fallow land and compared to the curve for mean air temperature.

In this area, wheat is seeded at a time close to the spring overturn when the soil temperatures are nearly uniform at 40°F. which is also a minimum temperature for wheat germination. Because of the early season, wheat roots apparently develop at less than optimum soil temperatures.

Corn planting is of necessity delayed until the soil warms up and the penetration of the working level of the root system corresponds to soil temperatures of about 60°F.

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ECOLOGICAL IMPLICATIONS OF CHANGES IN THE PHOTOSYNTHETIC RESPONSE OF *PINUS TAEDA* SEEDLINGS DURING ONTOGENY[1, 2]

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Developing *Pinus taeda* L. seedlings go through a series of stages marked by a shift in the predominance of different types of foliage. Immediately after germination, the cotyledons alone are the photosynthetic organs, but after a few weeks, the bulk of the foliage is made up of single, spirally arranged, juvenile (primary) needles. At approximately the middle of the first growing season, secondary needles began to develop in fascicles and by the beginning of the second growing season these form practically the whole of the foliage.

During investigations of the failure of pine to

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[1] This work was done with the aid of grants from the National Science Foundation (NSF—G909) and the Emory University Research Council.

[2] The author is indebted to the following members of the Department of Botany, Duke University: Professors P. J. Kramer and H. J. Oosting for reading the manuscript and to the former for permission to use the photosynthesis equipment in his laboratory; and Messrs. Vincent Schroeder and Howard Rock for their cooperation in making the measurements.

reproduce effectively under dense shade of pine or hardwoods, the photosynthetic response of two- and three-year-old seedlings with secondary leaves has been measured (Kramer and Decker 1944, Kramer and Clark 1947, Kozlowski 1949). These seedlings were found to be poorly adapted to conditions of low light intensity and this evidence was used to explain, in part, why pine seedlings ultimately fail under closed canopies (Kramer and Decker 1944, Kozlowski, 1949).

There is little information on the physiology of pine seedlings with juvenile foliage, yet as Goebel (1900) indicated, the morphologic and physiologic difference between juvenile stages and the adult form may be more or less great. It was thought that studies on seedlings with juvenile foliage might show a different photosynthetic response from that of seedlings with secondary foliage and might also account, in part, for the establishment of seedlings under closed canopies—a point not explained by the Kramer-Decker-Kozlowski hypothesis.

METHOD

To obtain information on the behavior of young pine seedlings with juvenile foliage, measurements of apparent photosynthesis were made during the summers of 1953 and 1954.

Exploratory measurements made on a few plants during 1953 indicated that seedlings with juvenile needles reached a maximum rate of photosynthesis between the relatively low light intensities of 1500 and and 3000 foot candles. For more precise information, additional measurements were made during August, 1954, on 16-week-old sun- and shade-grown seedlings with (a.) a mixture of juvenile and developing secondary needles (hereafter called intact seedlings), and (b.) juvenile needles alone, all secondary needles having been stripped from the seedlings one week earlier.

It was hoped that the first of these measurements would give data comparable to existing information on the photosynthetic reaction of older seedlings with secondary needles alone. The second measurement was designed to separate the contribution of juvenile and young secondary leaves to the total photosynthetic response of the seedling. In addition, these experiments were designed to test the preconditioning effect that development under full and partial light might have on the photosynthetic reaction of the seedling.

Another measurement was made during July on 10-week-old seedlings with juvenile needles. The data obtained are questionable because of technical difficulties encountered during measurement, but they approximate those presented later for 16-week-old seedlings.

General technique

Apparent photosynthesis was measured under controlled conditions of light, temperature, and carbon dioxide concentration in the closed system as described by Bourdeau (1954). Air in the closed system continually circulated over the plant at a rate of approximately 3 liters per minute. The time required to reduce carbon dioxide concentration from 10 per cent above normal (.03%) to 10 per cent below normal was taken as a measure of apparent photosynthesis. This reading was then converted to milligrams of carbon dioxide absorbed per hour (a) per plant and (b) per gram of oven dry weight of foliage. The converted data were statistically analyzed.

Light, regulated through the use of various combinations of wire screen and cheesecloth, was measured by holding the sensing element of a Weston Illuminometer at the point to be occupied by the central part of the seedling crown. The thin glass chamber was removed during these measurements, because it was assumed it would allow practically one hundred per cent light transmission.

Temperature, controlled by the cooling devices described by Bourdeau (1954), was maintained at 27±1° C.

The photosynthetic measurements were made in accordance with a random block design composed of 6 treatments (light intensities), 6 blocks (pairs of plants), and two pretreatments (sun- and shade-grown seedlings). According to this design, the apparent photosynthesis of 6 sun- and 6 shade-grown seedlings was measured under different light intensities (500, 1500, 3000, 4500, 6000, and 8500 foot candles) on consecutive days, a new light intensity being employed each day. Plants were chosen at random from the stock seedlings and randomly organized into pairs (blocks) composed of one sun- and one shade-grown seedling. Every pair appeared at each light intensity and at each time of day once.

Immediate preconditioning effects due to differential light conditions were minimized by keeping the experimental plants in a shaded room of the greenhouse for several days prior to and during the period of measurement. During this time, special care was taken to keep the plants well-watered. Seedlings were allowed 15 minutes to become adjusted to the light and temperature conditions within the chamber (Kramer and Decker 1944).

The seedlings, from seed collected in DeKalb County, Georgia, were grown in the Duke University greenhouse in three-inch clay pots filled with sandy soil. One-half of the plants developed under conditions of full sunlight, while the remaining half grew under a screen which reduced full sunlight to one-third intensity. One week prior to photosynthetic measurement, the plants in each light treatment were divided into two sub-groups: plants with many and plants with few secondary needles. The experimental plants were chosen at random from these sub groups: intact seedlings from the first and seedlings from which the secondary needles were removed from the second subgroup. At the termination of each measurement period, the following data were obtained for each experimental plant: the height of the stem from ground level; number of juvenile and secondary leaves; and oven-dry weights of root, stem, juvenile leaves, and secondary leaves (Table I).

TABLE I. Data on experimental plants

Seedling type	Pre-treatment	Height of stem (cm.)	Number of leaves		Oven dry weight (mg.)				
			Juv.	Sec.	Roots	Stem	Juv.	Sec.	Total
Intact seedlings	Sun	8.8*	138.2	43.0	202.8	87.1	149.8	119.9	559.6
	Shade	14.2	143.3	45.0	166.3	108.8	174.1	94.2	543.4
Seedlings with juvenile needles	Sun	7.2	156.0	—	213.7	83.7	237.1	—	534.5
	Shade	9.9	153.7	—	143.4	79.0	202.5	—	424.9

*Each figure represents a mean of six.

RESULTS

The results are presented in Tables II and III. All statistical analyses are on file at Emory University.

TABLE II. Average rates of apparent photosynthesis for intact seedlings as a function of light intensity

Light intensity (f.c.)	Milligrams of CO_2 absorbed per hour					
	Per plant			Per gram oven dry weight of foliage		
	sun grown	shade grown	sun + shade*	sun grown	shade grown	sun + shade†
500...	0.583	1.016	0.800	2.258	3.775	3.017
1500...	2.248	2.485	2.367	8.526	9.291	8.909
3000...	3.632	3.685	3.659	13.846	13.906	13.877
4500...	3.733	3.841	3.787	14.228	14.585	14.407
6000...	3.391	3.889	3.641	12.621	14.640	13.631
8500...	3.881	4.072	3.977	14.526	15.253	14.890

*0.919 indicates sig. diff. at 1% level.
†3.771 indicates sig. diff. at 1% level.

Comparisons based on milligrams of CO_2 absorbed per hour per plant and per gram of oven-dry weight of foliage indicated that in no instance was the difference in photosynthetic activity between sun- and shade-grown seedlings statistically significant.

Statistical analyses of the data for intact seedlings (Table II) showed significant differences between the photosynthetic rates at 500 f.c. and 1500 f.c. and between 1500 f.c. and 3000 f.c., but failed to show any significant differences between the reading at 3000 f.c. and those at higher light intensities. Apparently, the seedlings reached their maximum rate of photosynthetic activity at a light level between 1500 and 3000 f.c. and above this level further additions in light intensity had no significant effect on the rate of photosynthesis.

TABLE III. Average rates of apparent photosynthesis for seedlings with juvenile needles as a function of light intensity. (secondary needles removed)

Light intensity (f.c.)	Milligrams of CO_2 absorbed per hour					
	Per plant			Per gram oven dry weight of foliage		
	sun grown	shade grown	sun + shade*	sun grown	shade grown	sun + shade†
500...	0.446	0.540	0.494	1.913	2.676	2.295
1500...	1.684	1.652	1.668	7.230	8.145	7.688
3000...	3.035	2.661	2.849	13.325	12.848	13.087
4500...	2.281	2.210	2.246	9.731	10.711	10.222
6000...	3.126	2.658	2.892	14.198	13.321	13.760
8500...	3.349	3.292	3.321	14.571	16.015	15.293

*0.783 indicates sig. diff. at 1% level.
†3.71 indicates sig. diff. at 1% level.

Seedlings with secondary needles removed showed essentially the same photosynthetic response as intact seedlings (Table III). Significant differences were found between rates at 500 f.c. and 1500 f.c. and between 1500 f.c. and 3000 f.c., while the rate at 3000 f.c. was not significantly different from any at higher light intensities. However, the rate at 4500 f.c. was unexplainably low being significantly lower than the rate at 8500 f.c. and not significantly different than the rate at 1500 f.c.

A comparison of the general means of seedlings with and without secondary needles based on CO_2 absorbed per hour per plant indicated that the absolute rate of apparent photosynthesis was significantly higher for intact seedlings. This would be expected since the amount of foliage, both in numbers and weight of needles, was considerably greater on intact seedlings (Table I).

However, when this comparison was made on a unit basis (CO_2 absorbed per hour per gram of oven dry weight of foliage), the difference between seedlings with juvenile needles alone and intact seedlings was not significant. This is an indication that the presence of the first-formed secondary needles did not, on a unit basis, appreciably alter the photosynthetic response of seedlings. In other words, first-formed secondary needles are photosynthetically equivalent to juvenile needles. Since some of the first-formed secondary needles may have an internal anatomy similar to juvenile needles (Thompson 1914) and many others were not fully developed, this photosynthetic equivalence might be expected. Evidence presented later indicates that later-formed, fully developed, secondary needles are not photosynthetically equivalent to juvenile needles.

Discussion

The experimental data indicate that loblolly pine seedlings with foliage composed of juvenile needles, alone or mixed with developing secondary needles, reach maximum rates of photosynthesis at relatively low light intensities. This response is quite different from that of older seedlings with mature secondary needles as is shown by Fig. 1 where the response of 16-week-old and one- and two-year-old seedlings is graphed as a percentage of maximum photosynthesis.

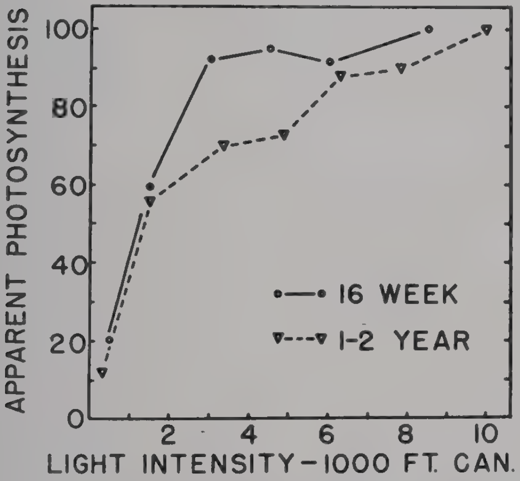

Fig. 1. Apparent photosynthesis (per cent of observed maximum) as a function of light intensity. Sixteen-week-old seedlings with a mixture of juvenile and first-formed secondary needles (Table II) and one- and two-year-old seedlings with mature secondary needles (Kramer and Decker 1944).

Sixteen-week-old seedlings reached their maximum rate of photosynthesis between 1500 and 3000 f.c. Additions of light beyond the 3000 f.c. intensity produced no significant increase in photosynthesis. In contrast, Kramer and Decker (1944) found that increases in light intensity from about 4700 f.c. to 9300 f.c. produced significant increases in the photosynthetic response of older seedlings with mature secondary needles. The data of Kozlowski (1949) on three-year-old loblolly seedlings are in accord with the findings of Kramer and Decker.

Young seedlings with juvenile needles are like seedlings of various hardwoods (Kramer and Decker 1944, Kozlowski 1949, Bormann 1953) in their ability to mtaintain maximum rates of photosynthesis under relatively low light intensities. As normal development of pine seedlings proceeds, however, and the foliage becomes dominated by mature secondary needles, maximum rates of photosynthesis can only be attained under the highest light intensities.

Among the factors responsible for the shift in photosynthesis associated with changing needle types, two seem to be important: an increase in the mutual shading effect and a lowered response to light due to a change in leaf anatomy.

Kramer and Clark (1947) using older seedlings found that individual secondary needles reached a maximum rate of photosynthesis at relatively low light intensities, while whole seedlings became light saturated only at the highest light intensities. The response of the entire seedling was attributed to mutual shading of the needles by one another. In older seedlings, mutual shading results both from the arrangement of needles in fascicles, and shading of the bottom of the crown by the top. The latter can be quite important as was indicated by light measurement made above (8000 f.c.) and below (2400-3800 f.c.) the crowns of two-year-old seedlings.

Mutual shading in seedlings with juvenile foliage is much less important because the crowns are smaller, and the leaves are borne singly in a spiral arrangement around an erect stem.

Basic differences in the anatomy of juvenile and secondary leaves may contribute to the changing photosynthetic response. Photosynthetic mesophyll tissue in mature secondary leaves is buried under three layers: a thick cuticle, an epidermis in which the cell walls are so thickened as to almost occlude the lucunae, and a hypodermis of one to several strata of thick walled sclerenchyma cells (Coulter and Chamberlain 1910, Esau 1953). Juvenile leaves are of simpler structure. Mesophyll tissue is covered only by a thin layer of cutin and a layer of relatively thin walled epidermal cells, while hypodermis is altogether missing (Masters 1891).

These anatomical differences suggest that the relatively thick outer covering of secondary needles screens out more of the incident light than does the thin covering of juvenile needles. Further, it seems probable that individual juvenile needles reach maximum rates of photosynthesis at lower light intensities than do individual secondary needles.

Indirect evidence of this may be obtained through a comparison of the relative rates of apparent photosynthesis for individual mature secondary needles and for entire seedlings with juvenile needles. The former reach a maximum rate of photosynthesis between 2250 and 3550 f.c. (Kramer and Clark 1947), while the latter achieve a maximum rate between 1500 and 3000 f.c. (Table III). Seedlings with juvenile needles seem to be photosynthetically more responsive (or at least equal in response) than individual mature secondary needles to low light intensities. Since there is some mutual shading in seedlings with juvenile needles, it follows that individual juvenile needles would achieve maximum rates of photosynthesis at lower light intensities than whole seedlings with juvenile leaves or individual mature secondary needles.

Another pertinent point is the comparative absolute rates of photosynthesis in juvenile and mature secondary leaves. Data from Table III when compared to data on oak (*Quercus*) and pine (Kozlowski 1949) indicate that juvenile leaves maintain absolute rates of photosynthesis equal to that of white oak leaves and approximately twice that of mature secondary needles. However, since these data were collected using different systems of measurement and since no provision was made to control translocation in either experiment, this comparison is inconclusive. It does indicate that this area should be experimentally explored.

Ecological Implications

The shift in the photosynthetic response of pine seedlings with ontogeny seems to have direct and meaningful applications to the role of the species in nature.

In the southeast, loblolly pine finds its best habitat in situations where conditions of relatively high light intensity prevail, particularly abandoned fields undergoing early succession. Although it can invade and colonize bare areas (McQuilken 1940, Bormann 1953), it frequently enters old field succession only after a dense cover of weeds or broomsedge (*Andropogon* spp.) is dominant. To be successful in these situations, the seedling must become established under the relatively low light conditions that prevail near the soil level, and later function successfully under the higher light conditions that exist in and above the upper layer of the dominant weed stratum.

Pine seems well-adapted to these progressively changing conditions. During the very critical period of establishment, its photosynthetic apparatus is able to function with relative efficiency under the prevailing conditions of low light intensity. As a consequence, it is probable that the seedling has a greater competitive ability and is better adapted to meet competition from the dominant weed vegetation. Later when the crown is composed of secondary needles the plant is taller and exposed to so much more light that its inability to utilize effectively lower light intensities is probably no great detriment.

The early establishment and later failure of pine seedlings under closed hardwood canopies may also be correlated with photosynthetic changes during ontogeny. Young pine seedlings with juvenile needles have a photosynthetic response similar to climax hardwood seedlings. This, combined with favorable weather conditions, probably accounts for their abundant establishment during some years. However, as development proceeds and the crown becomes composed of secondary needles, the seedlings lose their ability to photosynthesize efficiently under the unchanging low light intensities. Thus, they are unable to compete effectively with the more efficient existing vegetation and, as a result, they die out (Kozlowski 1949).

Summary

1. Loblolly pine seedlings, two or more years old, with secondary needles are known to be poorly adapted to conditions of low light intensity, however little is known of the response of younger seedlings with juvenile foliage.

2. Since information of this sort might be important in interpreting the behavior of seedlings during establishment, measurements of apparent photosynthesis were made on 16-week-old seedlings with juvenile needles alone and with a mixture of juvenile and secondary needles.

3. Both sets of seedlings reached maximum rates of photosynthesis at relatively low light intensities. In this respect, young pine seedlings with foliage dominated by juvenile needles were similar to hardwood seedlings and more efficient than older pine seedlings with secondary needles.

4, Increased mutual shading in older seedlings with secondary needles and basic differences in the anatomy of juvenile and secondary needles may account for the difference in photosynthetic response between seedlings with juvenile foliage and secondary foliage.

5. Although the first-formed secondary needles appear to be photosynthetically equivalent to juvenile needles, later-formed, fully developed secondary needles are thought to be less responsive to low light intensities.

6. The shift in the photosynthetic response of pine seedlings with ontogeny helps to explain the role of the species in nature.

(a) In old-fields, where pine thrives, young seedlings with foliage dominated by juvenile

needles are able to become established under the low light conditions that prevail near the soil under dense weed cover. Later when less efficient secondary needles predominate in the crown, the plant is taller and exposed to so much more light that its inability to photosynthesize efficiently under low light intensities is probably no great detriment.

(b) Under dense forest canopies, pine seedlings can become established because of their ability to utilize low light intensities. Later, when secondary foliage develops, seedlings are unable to photosynthesize effectively under the existing low light conditions. Thus they are unable to compete with the more efficient existing vegetation and, as a result, they die out.

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EVALUATION OF CERTAIN FACTORS AFFECTING THE YIELD OF CACAO IN ECUADOR[1]

ROBERT L. FOWLER, RUSSELL DESROSIERS, AND HENRY HOPP[2]

INTRODUCTION

It is often difficult to determine the importance of individual factors affecting the yield of an agricultural crop. This difficulty seems to apply particularly to cacao (*Theobroma cacao* L.) in Ecuador, where a number of factors in the growth of the cacao tree appear to overlap and modify one another. An attempt has been made in this paper to identify the most important of these factors and to determine the extent of their influence by means of a statistical analysis of data collected from 146 cacao haciendas during a survey of the Ecuadorian cacao industry in 1946 (Fowler and Lopez R. 1949).

The primary purpose of this cacao survey was to find superior cacao trees that might be developed into clones. During the course of the survey, however, various data pertaining to the yield of cacao, losses from disease, condition of the trees, cultural practices, and management of the plantations were collected.

ECOLOGICAL SETTING

The farms for which data were analyzed are located in Los Ríos and Guayas Provinces (Figure 1) which include the most important cacao producing area in Ecuador where more than one-half of the cacao exported from Ecuador originates. The original survey incluudes cacao plantings in the Provinces of El Oro and Manabí, but the analysis presented in this paper is based only on farms in Los Ríos and Guayas Provinces. This area lies in the broad, well-drained Guayas River valley on the coastal palin between the Andes Mountains on the east and a chain of disconnected low hills near the coast. Elevation increases from

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The authors wish to express their appreciation to Dr. John M. Aikman, of Iowa State College, formerly with the U. S. Operations Mission to Ecuador, and Mr. F. L. O'Rourke of the U. S. Operations Mission to Ecuador for their helpful comments during the preparation of the manuscript.

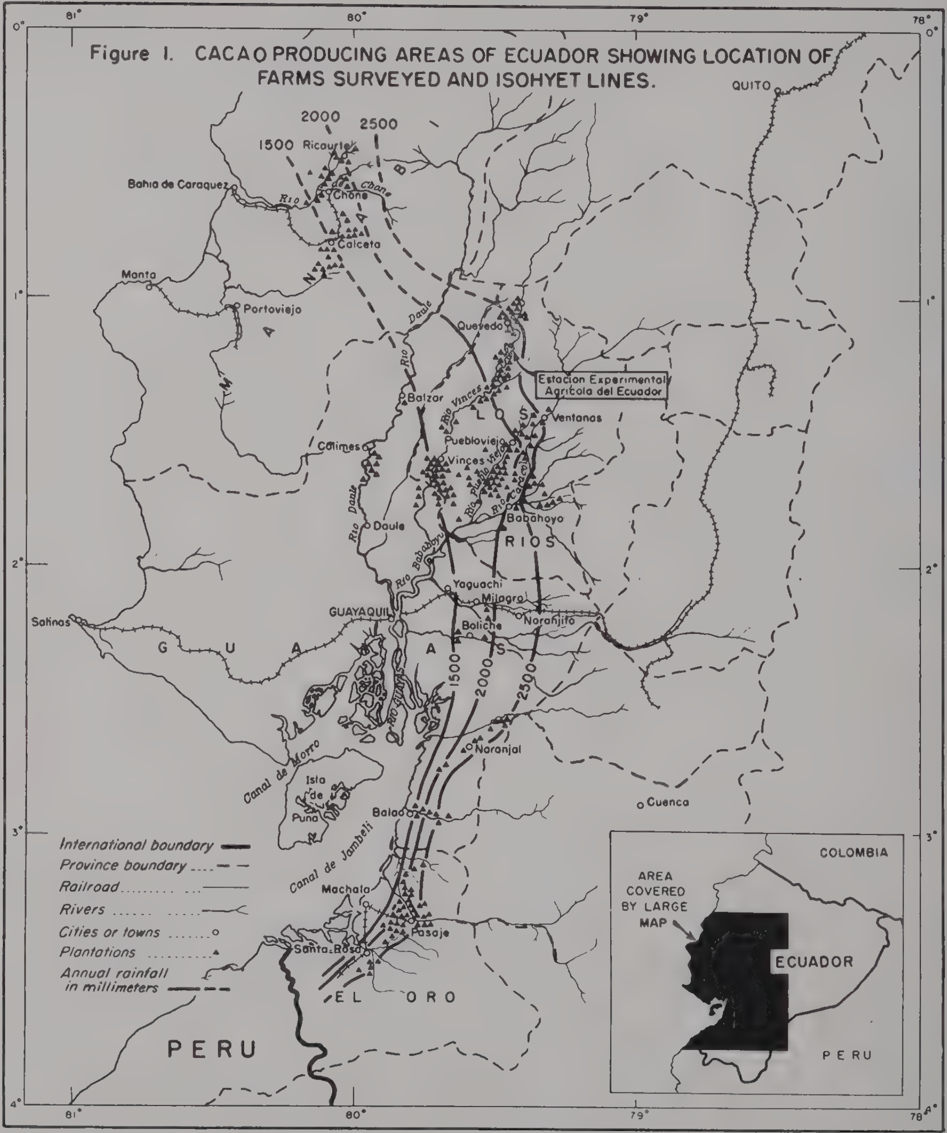

Figure I. CACAO PRODUCING AREAS OF ECUADOR SHOWING LOCATION OF FARMS SURVEYED AND ISOHYET LINES.

about 5 m. above sea level at Vinces to about 100 m. at Quevedo. Most of the soils of the region are fertile, deep, and alluvial in origin, and soil moisture is usually ample throughout the year.

The climate of the valley is remarkable in many respects. Although the Equator lies only one or two degrees to the north, the temperature remains quite moderate throughout the year. This equability is the result of a cloudy overcast that prevails during most of the year and reduces the impact of the sun's rays. Though constant during the dry season, from June to November, the overcast is frequently broken up during the rainy season. Because of this phenomenon, there are actually more hours of sunshine per day during the rainy season than during the dry. A mist, known locally as garúa, often occurs during the mornings in the dry season and is particularly heavy north and east of the 2,000 mm. isohyet. The combination of overcast and garúa provides favorable growing conditions for cacao and enables a semi-rainforest vegetation to persist in an area where otherwise it probably would not survive. Gentle breezes from a southerly direction prevail during the dry season and from a northerly direction during the rainy season. Strong winds are almost unknown.

Meteorological records for the region are fragmentary and few stations have records extending over very long periods. Enough data are available, however, to give a fairly reliable indication of conditions in the region (Table I and Figure 2). The isohyets on the map (Figure 1) were constructed on the basis of these data and data supplied by Molestina (1920-21) in his report of a meteorological survey of the coastal region.

TABLE I. Elevation and climate of five locations in the Guayas River Valley, Ecuador

Location	Elevation (m.)	Temperature, mean annual (°C.)	Rainfall, mean annual (mm.)	Relative humidity, mean annual (%)
Guayaquil	5	25.3	1,143.0	74
Milagro	13	25.5	1,437.7	89
Babahoyo	5	25.0	2,428.4	85
Vinces	5	24.0	1,234.1	80
Tropical Experiment Station (See Fig. 2)	91	25.0	2,400.0	88

Data from Vinces are from Proceedings of the Inter-American Technica Cacao Committee IV, Guayaquil, June 1952, published by the Empresa para la Renovación de Cacao, Guayaquil, Ecuador. Data for the Experiment Station are unpublished records of the Station. For other locations, various sources supplied data.

PLANTATION MANAGEMENT AND CULTIVATION

Two populations of cacao occur in the valley: Cacao Nacional and Trinitario (Cheesman 1944, Fowler 1952). The former is relatively homogeneous genetically and is the indigenous cacao population of the country; it is principally on this population that the reputation for high quality enjoyed by Ecuadorian cacao is based. Trinitario, a complex of segregating hybrids, is a relatively recent introduction.[3] Trees of Cacao Nacional are several times more numerous than are those of Trinitario.

Most cacao is grown along the river banks under the plantation system, with the plantings ranging in size from a few hectares to 1,500 hectares and averaging about 150 hectares. In most plantings, individual trees occupy an average area of about 12 sq. m., but in some they may occupy as little as 7 and in others as much as 25. Cultivation consists almost entirely of underbrushing one to three times annually. Spraying, fertilizing, and pruning are almost never practiced. Although cacao is harvested throughout the year, the principal crop is that of Cacao Nacional and occurs from February through May.

High shade is considered necessary for mature cacao and is provided by both native and introduced trees. In the highly humid regions close to the Andes Mountains, many of the shade trees are irregularly spaced jungle trees left standing when the land was cleared for cacao. Hence, some blocks of cacao on the same plantation are densely shaded whereas adjacent ones are poorly shaded or entirely exposed. In the drier regions, where most of the shade trees have been planted for the purpose, shade conditions tend to be more uniform.

PRINCIPAL DISEASES OF CACAO IN THE REGION

The two principal diseases occurring in the region are witches' broom, caused by *Marasmius perniciosus* Stahel, and Monilia pod rot, caused by *Monilia roreri* Cif. and Par.

Witches' broom attacks the vegetative shoots, the flower cushions (points on the trunk and branches where flowers appear), and the fruits (Baker and Crowdy 1943, 1944, Briton-Jones 1934). As a result of the death of "brooms" arising from new vegetative shoots attacked by the fungus, the disease may cause a reduction in photosynthetic tissue amounting to as much as one-third of the total foliage of the tree. This is in addition to the serious reduction in yield resulting from the destruction of pods directly attacked.

Monilia pod rot is a disease causing a moist rot of the pods and attacks no other part of the tree (Briton-Jones 1934, Rorer 1918). Cacao Nacional trees are rather uniformly susceptible to these diseases, whereas individuals of the Trinitario population, because of their hybrid origin, vary widely in susceptibility.

FACTORS SUBJECTED TO ANALYSIS

This analysis is based on data obtained as follows:

1. Yield. Pounds of dry cacao per hectare.
2. Rainfall. Mm. per year; estimated for each location from isohyets (Figure 1).
3. Witches' broom disease. Per cent of foliage killed by the disease; estimated by the grower and checked by inspectors visiting the farm.
4. Monilia pod rot. Per cent of crop destroyed by the disease as estimated by the grower.
5. Sunlight. Per cent of total sunlight falling on the trees; determined by estimating the density of shade (no shade, 100 per cent; light shade,

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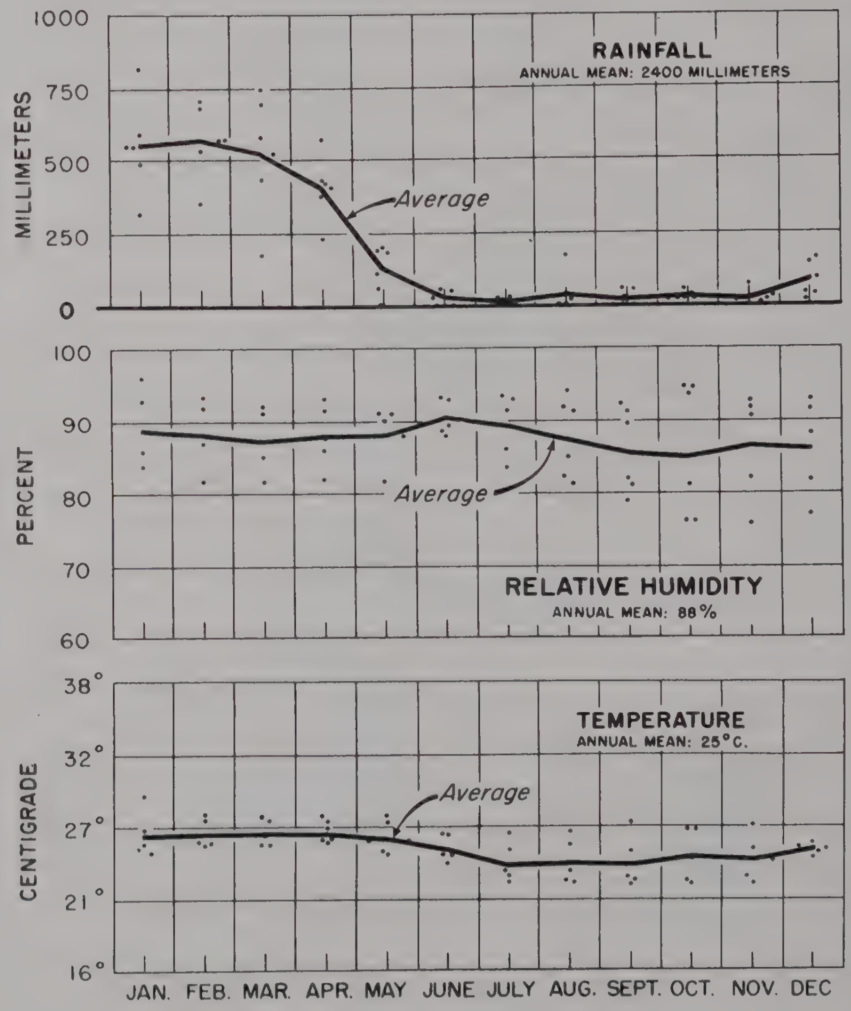
[3] Desrosiers, Russell. Genetic diversity of *Theobroma cacao* L. as a basis for selecting for resistance to witches' broom disease in Ecuador. Unpublished ms. in the files of U. S. Operations Mission to Ecuador.

Figure 2.

CLIMATOLOGICAL DATA FOR PICHILINQUE, ECUADOR 1944-1949 SIX YEAR MONTHLY AVERAGE



75 per cent; medium shade, 50 per cent; dense shade, 25 per cent).

6. Area of plantation in cacao. Hectares planted to cacao trees from which harvest was being obtained.
7. Area of land per tree. Square m. per tree, determined by examining a stand considered the average for each plantation.

RESULTS OF THE ANALYSIS

Effect of rainfall, witches' broom, and monilia pod rot

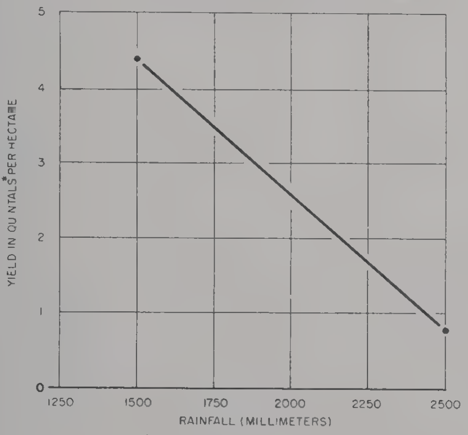
The rather complicated interrelationship among rainfall, witches' broom disease, and Monilia pod rot made it seem advisable, to consider these three factors as a group rather than to take each one separately. An examination of Table II will show the rather curious interlocking relationship of these three factors. A highly significant negative correlation is shown between yield and rainfall, and a significant correlation is shown between yield and witches' broom (see also Figures 3 and 4). The analysis shows no significant correlation between witches' broom and rainfall.

TABLE II. Correlation coefficients showing some of the associations among seven variables observed in 146 plantations in Los Ríos and Guayas Provinces, Ecuador

Variable	Yield	Witches' broom	Monilia pod rot
Yield	—	−0.21*	−0.09
Rainfall	−0.33**	0.14	0.38
Witches' broom	−0.21*	—	0.34**
Monilia pod rot	−0.09	0.34**	—
Sunlight	0.01	0.10	0.35**
Area of plantations in cacao	−0.30**	0.14	−0.05
Area per tree	−0.12	0.07	−0.13

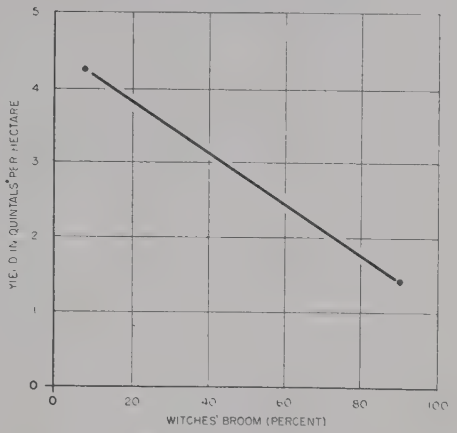
*Significant at the 5 per cent level.
**Significant at the 1 per cent level.

Figure 3.— RELATIONSHIP BETWEEN YIELD AND RAINFALL.



*ONE QUINTAL = 101.4 POUNDS

Figure 4.— RELATIONSHIP BETWEEN YIELD AND WITCHES' BROOM DISEASE.



*ONE QUINTAL = 101.4 POUNDS

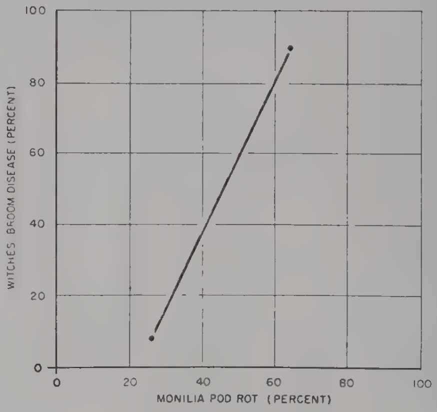
Excessive rainfall may have a deleterious effect on cacao by encouraging a luxuriant growth of weeds and by producing a temporary water-logging of the soil. Trees in the drier regions are noticeably less encumbered by epiphytes and vines than are those in areas of heavier rainfall. Considerable caution must be exercised, however, in interpreting the relationship between yield and rainfall. It should first be recalled that the variation in rainfall is related to the geographic locations of the plantations, a general increase in rainfall being noted from the coast to the foothill of the Andes Mountains (Figure 1). This means that the plantations receiving the greatest rainfall are also those that are farthest from the coast; therefore a part, at least, of the decrease in yield might be attributable to causes other than the heavy rainfall.

Effect of rainfall on yield is perhaps best interpreted as one element of a complex involving witches' broom disease and Monilia pod rot. Analysis of the data does not show a statistically significant correlation between incidence of witches' broom and amount of rainfall; but these data did not consist of actual counts of the "brooms" appearing in the trees. Rather, they were estimates of the per cent of foliage destroyed by the disease. Such estimates are subject, of course, to considerable error. This is suggested also by the fact that the effect of witches' broom on yield is significant only at the 5 per cent level. New flushes of vegetative growth on the trees would tend to obscure the dead "brooms" and would result in a low estimate; similarly, leaves killed by Diplodia twig blight, caused by *Diplodia theobromae* and defoliation by anthracnose, caused by *Colletotrichum gloeosporioides,* might be included in the estimate of witches' broom damage, thus making it unnaturally high.

A second source of error is that no consideration was given to losses in the form of pods directly attacked by the disease. Most pods killed by witches' broom become infected in the early stages of growth, being invaded either directly through stomata or systemically from the infected flower cushion (Dale 1946). Such pods never reach maturity and are likely to remain indefinitely on the trees as dwarfed mummies. That witches' broom does cause a loss by infecting pods directly is shown by Desrosiers, *et al.*[4] During a 23-month period, these workers counted all diseased and damaged pods appearing in the harvest from a stand of 147 Trinitario trees. They found that 17 per cent of the pods were infected with witches' broom. Although their study revealed an even larger per cent damaged by Monilia pod rot, they concluded that the effect of witches' broom was probably as great as, if not greater than, the effect of Monilia even without taking into consideration the additional effect of witches' broom on the vegetative part of the trees. The fact that most pods attacked by witches' broom are destroyed in the early stages of growth means that they represent a complete loss to the farmer. It is doubtful, however, that many farmers realize the magnitude of this loss and can make a good estimate of it. Most farmers are likely to be preoccupied with the pods approaching maturity and to overlook the inconspicuous mummies.

Although the survey data showed no correlation between witches' broom and rainfall, the sources of error may have been substantial enough to obscure such a relationship. That rainfall does have an important effect on the incidence of witches' broom is shown by Desrosiers and Bolaños.[5] These authors have plotted the rainfall by months with the number of dead brooms collected from 1,627 cacao plants under observation at the Tropical Experiment Station during 1951-1952. An examination of their graph shows that the amount of rainfall has direct influence on the number of brooms that develop on the plants during different seasons of the year. During 1951, when the rainfall was 2,724.4 mm., they collected as many as 29,444 brooms; whereas in 1952, when rainfall was only 1481.0 mm. they collected only 9,376 brooms. It is interesting to note that the difference in rainfall between the two years is about the same as that between the coastal and inland cacao producing areas (Figure 1). The serious effect of witches' broom on yield, indicated by the significant negative correlation between the two variables (Table II and Figure 5), seems to vary in intensity between the coastal and inland areas; and, it seems reasonable to assume that an important factor in this variation is the difference in rainfall between the two areas.

Figure 5.- RELATIONSHIP BETWEEN WITCHES' BROOM AND MONILIA POD ROT DISEASES.



Data from the 1946 survey showed a highly significant correlation between Monilia pod rot and rainfall. This relationship is borne out by data collected by Desrosiers, *et al.* at the Tropical Experiment Station from March, 1951, through November, 1954. Pods harvested during that time from the block of 147 Trinitario cacao trees mentioned previously were counted and the percentage that showed symptoms of Monilia infection was graphed with the rainfall of four months previous. The relationship between intensity of the disease and the amount of rainfall is striking. The graph suggests, however, that there may be a maximum level above which increased rainfall will not result in a corresponding increase in the intensity of the disease but may actually depress it. The highly significant correlation of Monilia with witches' broom that appeared in the analysis of the 1946 survey data (Figure 5) is probably just another indication that rainfall is favorable to the development of both diseases.

According to the data of 1946 survey, Monilia pod rot was not significantly correlated with yield. This lack of correlation may be explained by an insufficient variation in the amount of Monilia among the farms during the season when the estimates were made; or it may be explained as errors of estimation, for cacao growers show a definite tendency to overestimate losses from Monilia pod rot.

Only Monilia pod rot showed a highly significant correlation with the amount of sunlight. For this there seems to be no ready explanation except that it might be a chance relationship arising from the fact that the most carefully shaded cacao plantations lie closer to the coast, in the area of lighter rainfall, and the plantations uneven-

[4] Desrosiers, Russell, von Buchwald, Angel, and C. W. Bolaños. Relationship between rainfall and incidence of monilia pod rot of cacao in Ecuador. Unpublished ms. in files of U. S. Operations Mission to Ecuador.

[5] Desrosiers, Russell and C. W. Bolaños. Inhibition of sporophore development in *Marasmius perniciosus* Stahel on cacao by eradicant fungicides. Unpublished ms. in files of U. S. Operations Mission to Ecuador.

ly shaded by jungle trees lie farther inland, in the area of heavier rainfall. This explanation would link the correlation between Monilia pod rot and sunlight with the already established correlation between Monilia and rainfall.

Effect of area of plantation in cacao and of area of land per tree

A highly significant negative correlation appears between yield and area of plantation in cacao. This is to be expected, for it is the relationship that usually exists between extensive and intensive agriculture. On small plantations, labor is likely to be more closely supervised than on large plantations, and maintenance is usually better. Many of the large plantations have large areas in cacao that are difficult to reach and are given no attention except at harvest time. There is, however, a tendency towards larger plantations in the inland areas and smaller ones nearer the coast; and, part of the effect attributed to plantation size may actually be the effect of other factors already discussed.

Most cacao in Ecuador is much too closely planted, and a reduction in the stand of trees per hectare might logically be expected to result in an increase in yield. In this analysis, however, this effect did not appear. The lack of correlation between area per tree and yield might be due to there not being enough plantations with sufficiently reduced stands to make a mathematical relationship appear.

SUMMARY

An evaluation of certain factors affecting the yield of cacao in Ecuador is discussed. Among the factors considered are: amount of rainfall, incidence of witches' broom disease and Monilia pod rot disease, per cent of total sunlight falling on the cacao trees, area of plantation in cacao, and area of land per tree.

Correlation coefficients indicate a rather complicated interrelationship among rainfall, witches' broom disease and Monilia pod rot disease. A highly significant negative correlation is shown to exist between yield and rainfall, yield and witches' broom, and between yield and area of plantation. The data, however, indicate no correlation between yield and incidence of Monilia pod rot disease although Monilia pod rot disease is highly significantly correlated with witches' broom disease. An explanation is offered for this curious relationship as well as for the lack of correlation between Monilia pod rot and yield.

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THE DISTRIBUTION OF AQUATIC INSECTS IN TWO FLORIDA SPRINGS[1]

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INTRODUCTION

It has been previously noted (Berner 1950) that fewer species of immature aquatic insects are

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[1] This investigation was aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Florida (NR 163 106, Productivity of Florida Springs). I should like to acknowledge the invaluable aid and guidance of the following persons: my wife, Barbara Sloan, Drs. Lewis Berner, H. T. Odum, and the late W. C. Allee. For identification of various groups of insects, my sincere thanks to Drs. M. J. Westfall, R. F. Hussey, O. A. Johannsen, Messrs. Ellis Lanquist, and Robert Cumming. Dr. John H. Davis identified many aquatic plants and has provided estimates of vegetation densities. Mr. Elmo Reid, Manager of Homosassa Springs, and Mr. Ray Bullard, former Manager of Weekiwachee Springs, have been most cooperative. Mr. A. O. Patterson of the U. S. Geological Survey has provided valuable information on current velocities and temperatures in Weekiwachee Springs.

found per unit area at the sources, or boils, of spring-fed Florida rivers than in the rivers themselves. This phenomenon is by no means a local one. Ide (1935) found species gradients in the streams of Central Ontario as did Sprules (1947). Seurat (1922 *in* Brues, 1928) studied the species gradient in a large North African spring. These workers (with the exception of Berner) were investigating waters whose temperatures varied considerably even over small distances, and their conclusions that the insect distributions were in various ways correlated with temperature gradients were no doubt correct. Most Florida springs, however, by virtue of their large volumes of flow, maintain nearly constant temperatures over long distances from the sources. Solutions other than temperature gradients must therefore be sought to explain the distribution of insects in these springs. The present study is an attempt to determine qualitatively and quantitatively the extent of this differential distribution in two constant-temperature springs and their rivers, and to correlate the distribution patterns with measured environmental factors.

The constant-temperature springs of Florida provide their inhabitants with an environment of unusual stability. At any one point in a spring or its river the annual change in most measured chemical and physical factors is very small. The springs systems so far studied by H. T. Odum (1952, 1953, 1953a) indicate that they are, in fact, in steady states. This stability in time does not always, of course, extend to space; that is, gradients of certain environmental factors exist linearly in the rivers of the springs. The two major gradiently arranged elements whose effects were studied during the present investigation are chloride and dissolved oxygen.

The following terms will be employed throughout this paper. Since some of these are used in rather limited senses, their restricted definitions are given here.

Boil: that part of the spring, usually near the center of the pool, where the outflow actually occurs. This is generally marked by surface turbulence.

Pool: the remainder of the spring, or source, area.

Springhead: the area composed of the boil and its pool.

Run: the river of the spring.

Estuary: from the first part of the river to exhibit chloride fluctuations as a function of tidal effect, to the Gulf of Mexico.

Diel period: this refers to a section of time which includes one light (day) and one dark (night) period (Carpenter 1934 *in* Allee *et al.* 1949).

Throughout the following discussion, the term "springs" may be used to designate an entire river system. Whenever the source areas are specifically referred to, however, one of the above definitions will be used.

METHODS

The springs chosen for study were Homosassa Springs in Citrus County and Weekiwachee Springs in Hernando County, both on the middle west coast of Florida. These were selected because of their contrasting features and because of their relatively short rivers which could be travelled by boat in the space of half a day. The proximity of both rivers to the Gulf of Mexico, into which they flow, provided an opportunity to study the effects of chloride gradients and fluctuations due to tides on the aquatic insect populations.

Collecting stations were established at points in the rivers where decided differences exist in the environmental factors under consideration. Figures 1a and 1b are maps showing locations of collecting stations on both rivers. Collecting was done with a dip net containing 25 meshes per inch and having a bag opening of 13 x 10½ inches, a Ward's Needham scraper with a ⅛ inch mesh, and three strainer buckets having $\frac{1}{16}$, ⅛, and ⅜ inch mesh screens, respectively, and diameters of 9¼ inches. Collections were made at each spring about every six weeks from November, 1952 to February, 1954.

In order to determine the distribution of the various species in terms of occurrence frequency of their individuals, it was necessary that a reliable quantitative collecting method be devised. As quadrat studies in water of any depth are not necessarily accurate and are often very time consuming and since many of the forms encountered were vegetation dwellers which could easily be taken with a dip net, a prescribed number of dip net sweeps was taken as a composite standard sample. The number of sweeps necessary to obtain an adequate sample was determined in the following manner: By making single sweeps at random in the aquatic vegetation and then plotting the cumulative number of species collected against each increase in sampling area (successive sweeps), characteristic species-area curves were obtained. Three examples of these are shown in Figure 2. As can be seen, the curves have begun to level off to the left of five sweeps. The arrows indicate those points on the curves at which a 10 percent increase in sampling area results in only

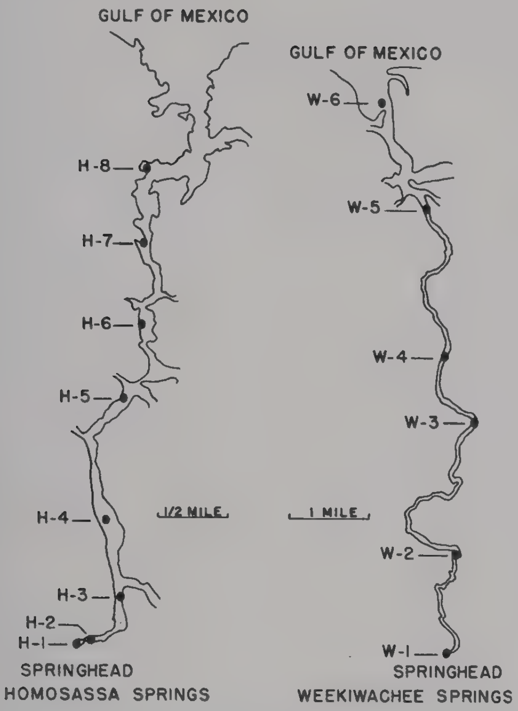

FIG. 1. Maps of (*a*, left) Homosassa Springs, and (*b*, right) Weekiwachee Springs, showing collecting stations. tions.

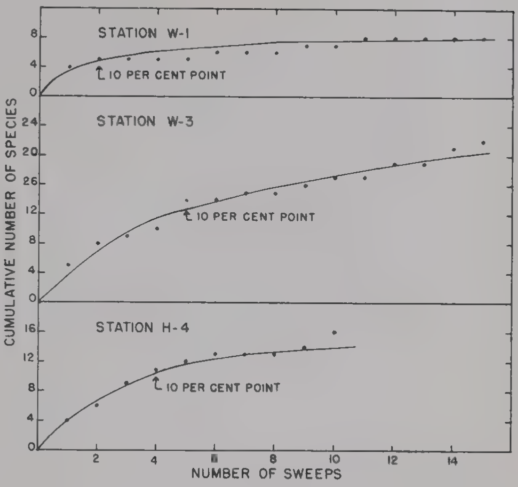

FIG. 2. Species-area curves showing minimum points of collecting adequacy.

a 10 percent increase in species number. This point was obtained by Cain's method (1938). It was assumed that sweeps in addition to five would be unprofitable and upon this assumption a five-sweep sample was adopted as the standard unit. Subsequently, when sampling quantitatively, at least five sweeps were made on each habitat. By applying analysis of variance to the data obtained in this fashion, it was possible to separate sampling error from actual variation in distribution.

Water temperature was measured with a standard centigrade mercury thermometer and was taken among the vegetation. Current velocity was determined with a Leopold and Stevens midget current meter and some values were also obtained from the U. S. Geological Survey, Surface Water Branch.

In order to determine the concentration of dissolved oxygen at maximum and minimum light intensity, water samples were taken among the plants during clear weather within the period 11 A.M. to 3 P.M. and before sunrise. The samples were fixed in the field and titrated upon returning to the laboratory. A test was made to determine the difference between results obtained using the Winkler method of analysis and the Rideal-Stewart modification of this method. Thirty water samples were collected from five stations in both rivers, and each method of analysis was used for half of the samples from each station. A total difference of 3.2 percent between the two methods was observed, with the Rideal-Stewart modification giving the highest values in all but one case. In view of this small difference and because of the slow procedure involved in the Rideal-Stewart modification, the Winkler method of analysis was employed throughout this study.

Chloride samples were collected at high and low tides as predicted by Coast and Geodetic Survey tide tables. Since samples were taken in the rivers and estuaries, however, and not on the coast, actual high and low tides were difficult to predict. Chloride analyses were made using the Mohr method.

The oxygen and chloride analyses were carried out as outlined in "Standard Methods for the Examination of Water and Sewage," 9th ed. (1946). Hydrogen ion concentration was measured by the color comparison method; bromthymol blue and cresol red were used as indicators. This was determined infrequently as other springs studies indicated that the pH variation with time at any one point was very slight.

HOMOSASSA SPRINGS

The Homosassa River has as its main origin Homosassa Springs, which is located on the Florida west coast in Citrus County about two miles west of U. S. Highway 19. It empties into the Gulf of Mexico after flowing five miles successively through mesic hammock, swamp, and coastal marsh. The boil area is utilized as a tourist attraction but neither swimming nor boating is allowed in this part of the river and consequently it is relatively undisturbed. An interesting feature of the boil is the large number of marine fish that congregate there. Odum (1953b) has suggested that these fish enter the boil from nearby feeding areas which are somewhat lower in chloride concentration and that the result of this movement may be a replenishing of their salt supply. At no point sampled in the entire river system does the chloride concentration fall below the lower limit of the oligohaline range (0.1 to 1.0 parts per thousand), and in the boil area the mean value found during this study is 0.74 $^{0}/_{00}$. The dissolved oxygen concentration in this region remains about 5 parts per million with extremely little variation during a diel period.

Around the edge of the pool, station 1, the dominant rooted aquatic plants are *Vallisneria neotropicalis, Potamogeton pectinatus* and *Najas guadalupensis* in that order of abundance. This part of the spring is scarcely disturbed by the current. As the water flows from the pool into the narrow channel, which at this point is about 15 yards wide, the current velocity approaches 0.5 ft/sec and the vegetation changes to predominantly *P. pectinatus.* Here *V. neotropicalis* and *N. guadalupensis* are found only in scattered patches. Up to this point, the bottom is composed about two and a half feet. The bottom now becomes softer and contains a large amount of partially decayed plant material which has a faint odor of hydrogen sulfide. Within one-half mile from the springhead, the current velocity has subsided to less than 0.3 ft/sec, the chloride concentration has become reduced to about 0.5 $^{0}/_{00}$ and the average dissolved oxygen has increased to approximately 7.5 ppm. The vegetation is composed mainly of *V. neotropicalis* having heavy epiphytic algal growths; smaller amounts of *P. pectinatus* are found in the deeper parts of the run. The width of the channel increases to about 150 yards. The river continues its broad, slow course with little apparent change for about one and one-half miles. The swamp through which the river has been flowing now rapidly gives way to saw-grass (*Mariscus jamaicensis*) marsh. This is probably the most inland part of the river to receive tidal water; the chloride concentration shows a daily fluctuation for the first time. At about this point, the water becomes more turbid; this turbidity increases downstream to the Gulf. The bottom here is composed of finely divided black silt, probably organic in origin, and the odor of hydrogen sulfide in the bottom material is considerably stronger than it was further upstream. The dominant rooted aquatics are *P. pectinatus* and *N. guadalupensis.* Within one mile the saw-grass is replaced by blackrush (*Juncus roemerianus*) and the silt, which was found overlying a very soft mud bottom in the saw-grass area, is now underlain by marine shell deposits. *Potamogeton pectinatus* is still the dominant rooted aquatic but *N. guadalupensis* and *V. neotropicalis* are found in small patches. These conditions persist for approximtaely two miles and then the marine alga *Sargassum* sp. becomes common and rooted aquatics disappear. This area is the farthest downstream from which collections were made. Table I summarizes the major physical features of each station in the Homosassa River. Current velocity refers to average surface velocity in the channel. The stations may be located by referring back to Figure 1a. The detailed data on chloride and dissolved oxygen concentrations, current velocity among plants, and pH may be found by consulting the section on Enviromental Features.

WEEKIWACHEE SPRINGS

This spring is located in Hernando County about twenty-five miles south of Homosassa Springs. The Weekiwachee River winds through nearly fourteen miles of scrub, swamp, and coastal marsh before flowing into the Gulf at Bayport, a resort village.

The springhead is situated about 100 yards west of U. S. Highway 19, and, like Homosassa, serves as a tourist attraction. Swimming is allowed in one section of the pool but this is confined to a small area some distance from the collecting station (station 1) and thus probably has little or no disturbing effect. The major features of this river system are in sharp contrast to those of Homosassa. The pool area is only sparsely covered by plants, the dominant rooted aquatic being *Sagittaria lorata.* The water movement to which the collecting site at the pool is subjected is that from the backwash of the boil. This is very slight. Unlike Homosassa, the chloride content is quite low in this area. The average concentration recorded during this study was 0.007 $^{0}/_{00}$, which is considerably below the oligohaline range. The dissolved oxygen has never been known to exceed 2.5 ppm in any part of the collecting station at the springhead, but, unlike Homosassa, may vary as much as 1 ppm during a diel period. The bottom is composed of firm, white sand not noticeably different from that of Homosassa except for color.

Two miles below the springhead the mean dissolved oxygen concentration has increased to about 4.5 ppm. The current is about 1 ft/sec and this remains nearly constant from the pool outflow

Table 1. Major environmental features of the collecting stations in Homosassa Springs. The abbreviations V. n., P. p., and N. g. stand for *Vallisneria neotropicalis*, *Potamogeton pectinatus*, and *Najas guadalupensis*, respectively

Station and miles from Boil	Dominant Submerged Rooted Aquatics			Temperature °C		Current Velocity (Surface of Channel)
	Order of Dominance	Percent Bottom Covered	Bottom Composition	Extreme Maximum	Extreme Minimum	Feet/Second
H−1 (0)......	V.n., P.p., N.g.	30	Fine yellow sand	23.3	22.5	Less than 0.01
H−2 (.20)....	P.p., N.g., V.n.	50	Above type plus areas topped with organic detritus	24.0	22.8	0.53
H−3 (.70)....	V.n. with heavy algal growth	40-50	Sand and silt topped with organic detritus	24.9	22.0	0.27
H−4 (1.5)....	P.p., N.g., V.n.	70	Sand topped with fine black silt. H_2S odor	26.2	23.9	0.13
H−5 (2.0)....	P.p., N.g., V.n.	30	Organic detritus and black silt. H_2S odor	27.8	20.0	0.19
H−6 (3.0)....	P.p., V.n., N.g.	15	Black silt merging into silt-covered shellbar	29.0	19.0	Less than 0.01
H−7 (4.0)....	P.p., V.n., N.g.	10-15	Shellbar covered with black silt. H_2S odor	29.0	18.5	Less than 0.01
H−8 (4.5)....	Sargassum sp.	5-10	Shellbar covered with black silt. H_2S odor	....	17.5	Less than 0.01

to the estuary. The channel width varies from approximately thirty to fifty feet for the entire course of the river. The average depth of the entire run is estimated to be about five or six feet. The dominant rooted aquatics are *S. lorata* and *Najas guadalupensis* and the bottom ranges from firm, white sand to soft, black silt and organic detritus. Six miles down the run (station 4) the situation is much the same except that *N. guadalupensis* has replaced *S. lorata* as the dominant rooted plant, and the average dissolved oxygen concentration has increased to 7 ppm.

The next noticeable change occurs starting at a point about nine miles from the springhead. Here the tidal effect, as evidenced by increasing chloride concentrations, first becomes obvious. This is reflected in the changing vegetation. *Potamogeton pectinatus* first appears and *S. lorata* slowly becomes replaced with *Vallisneria neotropicalis* while *N. guadalupensis* becomes increasingly sparse. The swamp, through which the river has been flowing, changes abruptly to saw-grass marsh which merges quickly into black-rush marsh. The bottom ranges from white sand to soft, brown silt. The river now enters the area of estuarine conditions where *P. pectinatus* is dominant, although *V. neotropicalis* and a small amount of *Najas* are still found. The current slows to less than 0.1 ft/sec as the estuary broadens, and the depth is reduced to three to four feet. The bottom now consists of sand mixed with finely divided, black silt which has a strong hydrogen sulfide odor. Just before the open Gulf is reached, *P. pectinatus* is replaced with *Ruppia maritima* and the other rooted aquatics disappear. At high tide, the chloride concentration here (station 6) approaches one third that of sea water.

The major physical features of each station in Weekiwachee Springs are shown in Table II and the stations may be located in Figure 1b. The chloride and dissolved oxygen concentrations for each station are discussed and graphed in the section on Environmental Features.

Major Environmental Features

The major environmental factors studied during this investigation were concentrations of dissolved oxygen and chloride. Gradients of these are present in both river systems but differ considerably in each. Temperature and pH were measured only occasionally since a study made by the Florida Geological Survey (Furguson *et al.* 1947) indicated that these features are remarkably constant for springs in general. Current velocities were measured infrequently. The five environmental factors cited above will be discussed in the following paragraphs.

Homosassa Springs

DISSOLVED OXYGEN. Figure 3 shows the mean dissolved oxygen and the change in dissolved oxygen concentrations at the collecting stations in the Homosassa River. Mean dissolved

Table II. Major environmental features of the collecting stations in Weekiwachee Springs. The abbreviations S. l., N. g., P. p., V. n., and R. m stand for *Sagittaria lorata, Najas guadalupensis, Potamogeton pectinatus, Vallisneria neotropicalis,* and *Ruppia maritima,* respectively

Station and miles from Boil	Dominant Submerged Rooted Aquatics		Bottom Composition	Temperature °C		Current Velocity (Surface of Channel)
	Order of Dominance	Percent Bottom Covered		Extreme Maximum	Extreme Minimum	Feet/Second
W−1 (0)......	S.l. with some epiphytic algae	10-15	White sand covered sparsely with plant detritus	24.0	23.2	Less than 0.01
W−2 (2.0)....	S.l., N.g.	30	From firm white sand to black silt and detritus	25.3	23.3	0.90
W−3 (6.4)....	N.g., S.l.	45	Same type as W−2	26.0	19.0	0.90*
W−4 (8.5)....	N.g., S.l.	30	Same as W−2 except silt lighter in color	28.0	18.0	0.72
W−5 (11.7)...	P.p., V.n., S.l. (drops out in this station), N.g.	15-25	From fine white sand to brown silt	28.0	....	....
W−6 (13.6)...	V.n., P.p., N.g., small amount of R.m.	30-40	Sand mixed with black silt. H_2S odor	30.8	15.7	Less than 0.01

*Average of USGS cross-sectional values.

oxygen is the average of mean day and night values and dissolved oxygen change is the mean day minus the mean night value. Figure 3 also shows all of the actual values recorded at the stations.

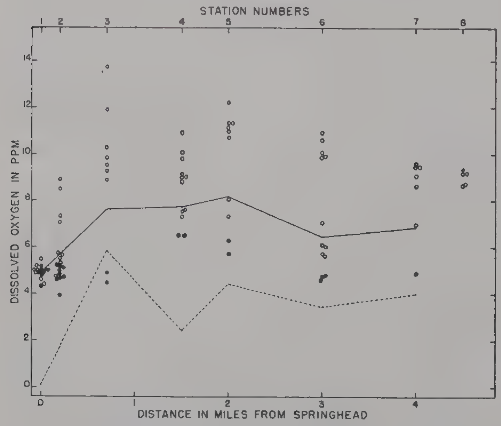

Fig. 3. Dissolved oxygen concentrations in Homosassa Springs. Black points are night values, open points day values. Solid line, average of mean-day and mean-night values; dotted line, difference between mean-day and mean-night values.

The dissolved oxygen concentration of the boil and pool is relatively high compared to springs such as Weekiwachee and Silver (Odum 1953). No value below 4.3 ppm was recorded from this station (station 1) during the study. Like the headwaters of many other Florida springs, a striking feature connected with dissolved oxygen is the nearly constant concentration exhibited through a diel period. Apparently the water, which has just emerged from subterranean crevices and is fairly homogeneous with respect to dissolved oxygen concentration, is not in contact with the plants of the pool area for a sufficient length of time to allow an increase in dissolved oxygen content due to photosynthetic activity to occur. Similarly, during the dark period, the respiration effect is not reflected in a dissolved oxygen decrease.

As the channel narrows and approaches station 2, the water becomes more turbulent and diffusion may take place more readily. The rooted aquatic plants increase in density and the photosynthetic and respiratory potentials per unit area thus increase. These three effects, diffusion, photosynthesis, and respiration, are reflected in the higher average dissolved oxygen concentration and a larger change per diel period. The environment here, at least with respect to dissolved oxygen, is decidedly less constant than that of station 1.

At station 3, there is no turbulence and the current is so slight as to be immeasurable by the method employed. The growth of rooted aquatics is heavy and the epiphytic algal growth is extremely dense. These algae, mostly *Cladophora* sp., sometimes completely cover the upper side of the leaves of *Vallisneria* plants, which are dominant at this station. Although growths of epiphytic algae are common in most parts of the run, they are nowhere else nearly so luxuriant as at this station. Among the plants, dissolved oxygen is sometimes found in concentrations exceeding 13 ppm and it is at this station that the most variable dissolved oxygen concentrations have been recorded per diel period for the entire river system.

At station 4, the mean night dissolved oxygen concentraton is considerably higher than that of station 3 while the mean day dissolved oxygen content is lower. The fluctuation in dissolved oxygen concentration is thus less than at station 3.

At station 5 the average dissolved oxygen concentration is higher than at station 4. The rooted aquatic coverage is less as is the epiphytic algal growth, so the increase is probably not a function of local photosynthetic activity. The current is comparable to that of station 4 and there is no observable turbulence.

Station 6 has generally lower dissolved oxygen concentrations than the preceding station. The smaller values may be a function of the increased salinity (Sverdrup *et al.* 1949), the larger amounts of organic matter as evidenced by the increased turbidities, the decrease in aquatic plant density, or a combination of these. The diel change in dissolved oxygen is somewhat less than at station 5 though not markedly so.

The tendency toward lower dissolved oxygen concentrations seen at station 6 continues through stations 7 and 8 (see Figure 3). Due to the difficulty of reaching station 8 before sun-up, minimum dissolved oxygen values were never obtained from that area; however, the diel change in dissolved oxygen is probably about the same as at station 7.

CHLORIDE. Figure 4 shows the actual chloride values recorded at each station. These are enclosed in histogram fashion so that the extent of fluctuation may easily be seen. Although most of the chloride samples were taken at high and low tides as given in the U. S. Coast and Geodetic Survey Tide Tables, these designations apply only to the point at which the estuary meets the Gulf. Consequently, there is considerable lag between apparent and actual tide stages in the estuary itself. At stations 7 and 8, high tide water was apparently never sampled although several attempts were made to do so, and the tidal fluctuation is no doubt greater than is shown in Figure 4. The maximum chloride values from these stations are not known but it would seem that they should be in excess of those at station 6, whose maximum recorded value was 5.1 $^{0}/_{00}$.

At the river's source, station 1, the chloride content averages 0.74 $^{0}/_{00}$. This high concentration comes from ground water and is not due to marine tidal invasion (Odum 1953b). The fluctuation in concentration is probably due to dilution of groundwater after periods of rain.

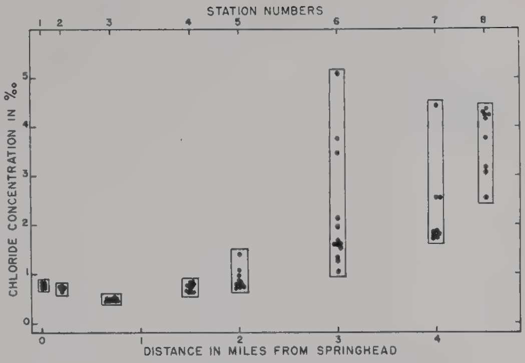

FIG. 4. Chloride values in Homosassa Springs.

Although station 2 shows a slight drop in chloride concentration, which may not be significant, the range of fluctuation is about the same as at station 1. If the drop represents a real decrease, it may indicate that there are other, fresher springs contributing to the river somewhere between stations 1 and 2.

The concentration at station 3 is still lower, and the values here show less fluctuation than the previous two stations. The variation between maximum and minimum values obtained from eleven samples taken at different apparent tide stages was 0.048 $^{0}/_{00}$.

Between stations 3 and 4 a stream known locally as the Hall River flows into the run of Homosassa. The three water samples obtained from the channel of this river contained 1.15, 1.77, and 1.76 $^{0}/_{00}$ chloride. The inflow of this brackish water probably explains the rise in chloride concentration from station 3 to 4. The fluctuation here is possibly due to incomplete mixing of the slightly brackish water from upstream and the more brackish water from the Hall River. The maximal values recorded from station 4 are the same as those from the boil while the minima are somewhat lower.

Station 5 is probably the first station to receive tidal water of marine origin; the tidal effect here produces an observed fluctuation of 0.67 $^{0}/_{00}$ chloride. For the purpose of this study, the estuary begins at this station. Figure 4 shows the large increase in fluctuation that takes place between stations 5 and 6. The minimum chloride values steadily increase through station 8 although the maximum values seemingly decrease past station 6. As mentioned in the opening paragraph of this discussion, this is probably because the last two

TABLE III. pH values at collecting stations in Homosassa and Weekiwachee Springs

	H−1	H−2	H−3	H−4	H−5	H−6	H−7	H−8	W−1	W−2	W−3	W−4	W−5	W−6
November 1953......	7.5	7.5	7.5	...	7.7	8.4	8.1	8.1	...	7.5	7.4	7.4	7.4	...
February 1954.......	...	7.7	7.6	7.6	7.7	8.0	8.0	8.3	7.6	...	7.6	7.6	...	7.5

stations were apparently not visited during actual high tide; therefore, the true maximal values are probably considerably in excess of the concentrations shown.

CURRENT VELOCITY. Because of mechanical difficulty encountered in using the current meter, only two series of velocity measurements were made. The values in Table I are averages of these and refer to surface velocities in the channel. The lowest reading that the meter will register is 0.01 ft/sec. Therefore, where no current was encountered it is reported as being less than 0.01 ft/sec.

At station 1, the backwash from the boil is the only observable current to which the inhabitants of the pool edge are subjected. This is very slight and not at all obvious. As the water flows from the pool toward station 2, however, the current quickly increases to an average of 0.53 ft/sec. Since the channel is narrow and there are no protected areas, all parts of the station are subjected to current of this average velocity. By the time the river has progressed to station 3, the mid-channel velocity has decreased to an average of 0.27 ft/sec and the current among the plants at the collecting site is less than 0.01 ft/sec. The current velocity at station 4 is again less than 0.01 ft/sec among the plants and averages 0.13 ft/sec in the channel. At station 5 the velocity averages 0.08 ft/sec among the plants and 0.19 ft/sec in the channel. The velocity reported for station 5 must be viewed with some reservation, however, because on one occasion the "current" was seen to be flowing upstream. This was probably due to a combination of backing up of water from the incoming tide and a strong wind which was blowing in an upstream direction. Station 5 was the last station at which velocities were measurable. The current at stations 6, 7, and 8 are therefore considered to be less than 0.01 ft/sec., although during incoming and outgoing tides and periods of high wind, these stations are probably subjected to a slight irregular current.

HYDROGEN ION CONCENTRATION. Since a survey of all the major Florida springs by Furguson *et al.* (1947) showed the variation of pH to be slight for springs in general even over long periods of time, only two series of pH readings were made at each station. Like most other Florida springs, Homosassa is alkaline due to the leaching of its waters through limestone before reaching the surface. Table III shows the pH values at each of the stations for the two series taken during this study. The fluctuations shown in this table for stations 1, 2, 3, 4, and 5 are small enough to be within the range of reading error. The variation between values at stations 6, 7, and 8 is probably due to the changes in chemical composition of the water with high and low tides. A correction for salt-error was applied to stations 6, 7 and 8 using the correction factors employed by Harvey (1928).

TEMPERATURE. Temperatures were recorded among the plants with a centigrade mercury thermometer. Table IV shows values which were recorded over a nine-month period. Stations 1, 2, and 3 are seen to approach constant temperature while the lower stations, although varying somewhat between summer and winter months, still have at the most a ten degree change between these seasons.

TABLE IV. Water temperature values (°C) recorded at collecting stations in Homosassa and Weekiwachee Springs

	June 1953	July 1953	Aug. 1953	Oct. 1953	Nov. 1953	Jan. 1954	Feb. 1954
H−1.......	23.2	....	....	....	22.5	23.3	...
H−2.......	23.3	....	23.5	....	24.0	....	24.0
H−3.......	24.0	....	....	....	22.0	23.3	24.9
H−4.......	....	....	26.2	....	....	....	23.9
H−5.......	27.0	....	27.8	....	20.0	....	22.5
H−6.......	27.0	....	29.0	....	19.0	....	22.0
H−7.......	....	....	29.0	....	18.5	....	20.3
H−8.......	....	....	....	....	17.5	....	20.8
W−1......	....	24.0	23.5	23.5	....	23.9	24.0
W−2......	24.0	24.6	23.5	24.8	....	....	....
W−3......	26.0	26.0	....	....	....	....	23.5
W−4......	26.0	28.0	27.0	22.5	....	18.0	22.4
W−5......	27.0	28.0	....	..	....	....	....
W−6......	27.4	30.8	....	24.8	....	15.7	20.5

WEEKIWACHEE SPRINGS

DISSOLVED OXYGEN. Figure 5 shows the mean dissolved oxygen concentrations and changes in dissolved oxygen at the collecting sites in the Weekiwachee River system, and also indicates the actual values recorded at these stations.

The dissolved oxygen of the headwaters of this spring is among the lowest of the non-anaerobic

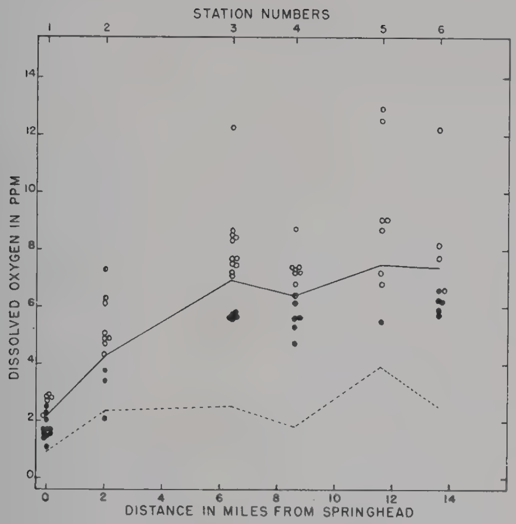

FIG. 5. Dissolved oxygen concentrations in Weekiwachee Springs. Black points are night values, open points day values. Solid line, average of mean-day and mean-night values; dotted line, difference between mean-day and mean-night values.

Florida springs. The mean dissolved oxygen concentration is 2.20 ppm and, unlike Homosassa which has practically no diel fluctuation, has a dissolved oxygen change of almost 1 ppm. This is probably because Weekiwachee has a larger pool and the water from the boil, instead of flowing immediately to the run, as in Homosassa, can stand at the edge for some time. This water may then be acted upon by photosynthesis and respiration. The fluctuation is still small, however, in comparison with many other aquatic situations, and the environment in the pool (station 1), in terms of dissolved oxygen, is still unusually constant. At no other known point in the river does the dissolved oxygen descend to the level of that of the springhead.

At station 2, although this is two miles below the river's source, the mean dissolved oxygen concentration has increased only to 4.3 ppm with mean minima and maxima of 3.08 and 5.46 respectively. The minimum values used for this station were obtained from samples collected on rainy days since night water samples were very difficult to obtain in this part of the river. The low concentration found here is probably due to the fairly low densities of rooted aquatics throughout the two mile course. Even though the dissolved oxygen content remains low at this station, the diel fluctuation as shown in Figure 5 is considerably greater than that of the previous station.

The steady increase in dissolved oxygen content continues through station 3, the mean here being almost 7 ppm. The diel fluctuation, 2.55 ppm, is slightly greater than that of station 2. One very high value was recorded from this station (see Fig. 5). This sample was probably taken in water that had somehow been standing long enough among plants, perhaps in a small whirlpool, to become supersaturated with respect to oxygen.

Station 4, whch is approximately two miles below the previous station, shows a slight drop in mean dissolved oxygen content. This may be a reflection of the 15 percent decrease in plant density. Compared to station 3, this station exhibits a fairly large drop in diel fluctuation of dissolved oxygen.

No water samples were collected from station 5 during the dark hours but the one rainy-day sample taken probably approaches the night concentration. The mean day values are generally high compared to upstream stations even though there is a large decrease in plant density.

Station 6 is located in the broad, shallow bay shown in Figure 1b. The aquatic plant growth is very dense in parts of this area and the dissolved oxygen concentration is correspondingly high; not so high, however, as at station 5. The chloride content of the water at high tide becomes almost a third that of sea water but this seems to have little effect on the dissolved oxygen concentration. The change in dissolved oxygen per diel period is somewhat less than at station 5.

CHLORIDE. Figure 6 shows chloride values from all stations. These, as in the chloride diagram of Homosassa Springs, are enclosed in order to show ranges in fluctuation.

Stations 1, 2, and 3 are definitely in the fresh water range. None of these stations reach the "nearly oligohaline" (Odum, 1953b) range of 0.025 to 0.100 $^{0}/_{00}$. The fluctuation shown at all these stations is very small and probably within the range of experimental error.

Station 4 shows a slight increase in chloride content over the previous three stations. On two occasions, values falling in the "nearly oligohaline" range were recorded. There is a possibility that this increase is due to inflow of water of marine origin, but the distance of this station from the Gulf and the high current velocity throughout the entire run would seem to indicate that this is not the case.

Station 5 shows a definite chloride fluctuation and this is no doubt due to marine tidal water. During low tide the chloride content at this station is comparable to that of station 4. However, one sample indicates that at high tide the concentration increases well into the oligohaline range.

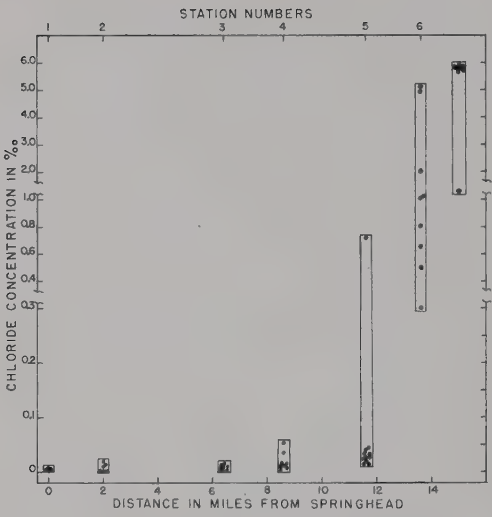

Fig. 6. Chloride values in Weekiwachee Springs.

At station 6, the concentration during high tide becomes nearly one third that of sea water. At low tide, however, values in the low oligohaline range have been recorded. The measured extremes in chloride content at this station are 0.30 and 5.28 ‰. The last block of values in Figure 6 are from samples taken at the mouth of the river about one-eighth of a mile from station 6. These values range from 1.3 to 5.8 ‰.

CURRENT VELOCITY. Table II shows the surface current velocity in the channel at the various stations. Since these (with the exception of the U. S. Geological Survey readings) are averages of measurements made at the same time, no information is available on fluctuation of current velocity throughout the year. However, the USGS values show that cross-sectional averages taken ¾ mile downstream from the springhead range from a low of 0.75 ft/sec in November, 1952 to 1.12 ft/sec in June, 1953. The values shown in Table II are probably comparable to the current to which the plants and their inhabitants are subjected since all collecting sites were in areas which are exposed to current.

No measurable river current was found in the bay, but upon one occasion a water velocity of 0.34 ft/sec was recorded flowing into the estuary. This was during the tidal inflow. Apparently this area, like that of Homosassa, is subject to reversal of current with change in tidal flow and wind direction.

HYDROGEN ION CONCENTRATION. pH was measured in the same manner as for Homosassa. A correction for salt-error was made for station 6. Table III shows the two series taken during this study. These seem very similar to the values recorded in Homosassa except for the estuary samples.

TEMPERATURE. Table IV shows temperatures as recorded over a nine-month period. There is practically no temperature fluctuation until station 3 is reached, and even then the observed seasonal variation is less than three degrees. The bay shows the greatest range of seasonal fluctuation, slightly in excess of fifteen degrees. This is somewhat more than for the Homosassa estuary.

Species Distribution and Population Density

Previous mention has been made of the occurrence of smaller numbers of species in spring pools in comparison with the runs. It is also true that there are fewer individuals in these source areas than in the runs. In the following discussion estimates of relative density for those species whose populations were not quantitatively measured are necessarily somewhat arbitrary. General estimates will be given for some of these species, however. Species distribution in Homosassa and Weekiwachee Springs is shown in Figures 7 and 8; Figure 9 shows the species distribution broken down to orders. Because of its length, a table showing the species present at each station is omitted. This information is available in thesis form in the University of Florida libraries. Dissolved oxygen and chloride concentrations at the collecting sites are shown in Figures 3 through 6.

Population density in this study refers to the mean number of individuals collected per unit area. Actual numbers of insects collected were used in calculations of population density. Only two groups, the Ephemeroptera and Odonata, were studied from a quantitative standpoint since the structural adaptations of other groups, such as

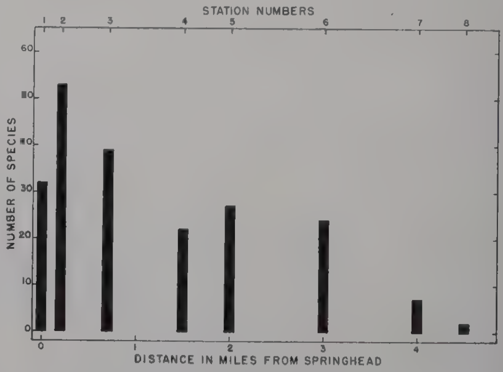

Fig. 7. Numbers of insect species taken from collecting stations in Homosassa Springs.

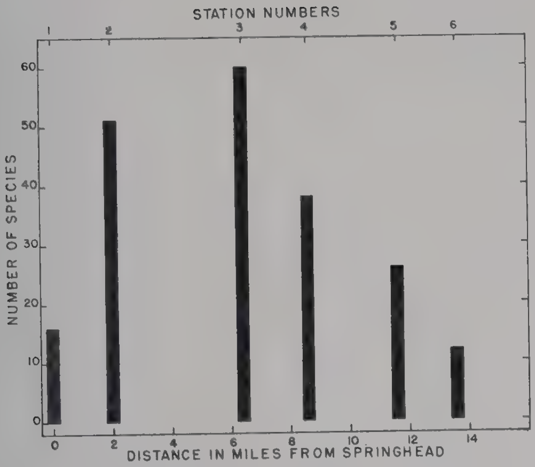

Fig. 8. Numbers of insect species taken from collecting stations in Weekiwachee Springs.

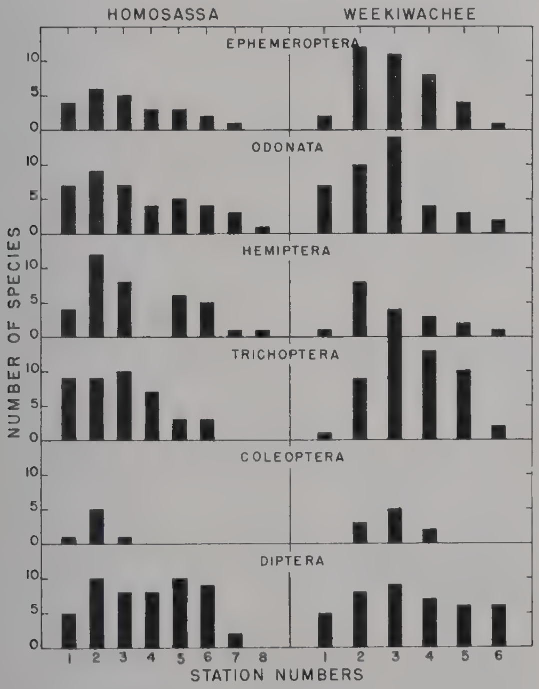

Fig. 9. Number of species per order of insects taken in Homosassa and Weekiwachee Springs.

the vegetation-adhering cases of the Diptera and Trichoptera, would not permit a valid numerical comparision of their populations with those of the first two groups mentioned without devising other collecting methods. The mean number of individuals per sweep, shown in Figures 10 through 13, was determined by dividing the total number of individuals collected by the number of sweeps made at that station. The values shown in these figures are based on a total of 697 sweeps.

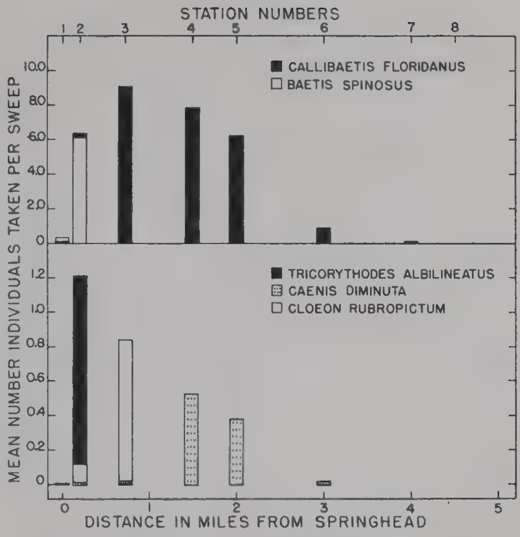

Fig. 10. Relative population densities of five species of mayflies. Homosassa Springs.

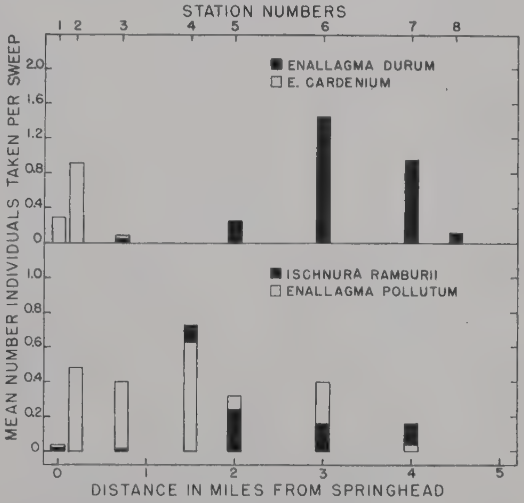

Fig. 11. Relative population densities of four species of damselflies. Homosassa Springs.

Homosassa

DIPTERA. In the omitted table, mentioned above, some of the dipterous forms were grouped into categories higher than species. For the purpose of this study, the Chironomidae include all forms in this family with the exception of the Chironominae and the Tanypodinae, since these were considered separately. The Chironominae include all of the genus *Tendipes* (= *Chirono-*

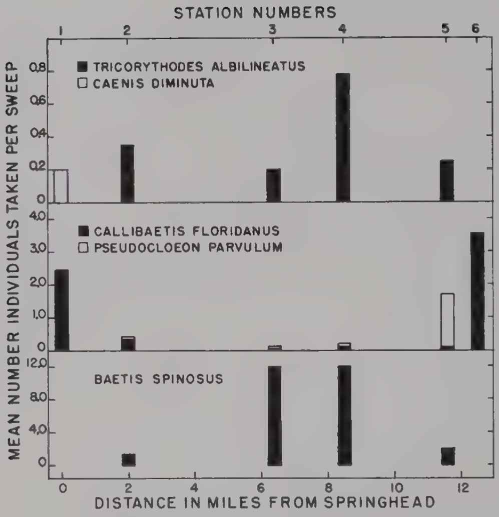

Fig. 12. Relative population densities of five species of mayflies. Weekiwachee Springs

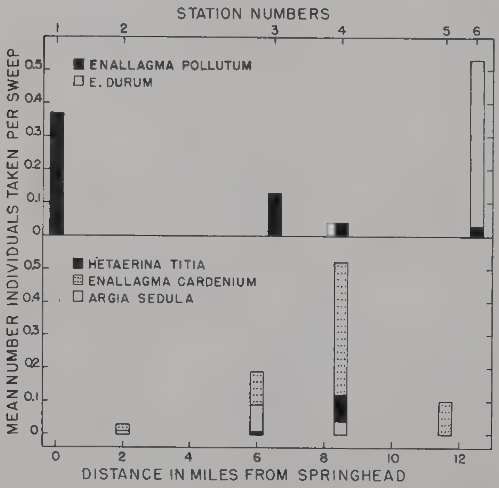

Fig. 13. Relative population densities of five species of damselflies. Weekiwachee Springs.

mus) with the exception of the *Tendipes decorus* and *T. militaris* groups. The Tanypodinae include all those in this subfamily. *Tanytarsus* includes all members of this group. The above mentioned forms, along with the *Palpomyia* and *Bezzia* groups, are very evenly distributed in the Homosassa River.

None of the groups mentioned above are found in large numbers at any station but seem to be present in smaller numbers in the pool (station 1) than at other stations. As might be expected, the predaceous Tanypodinae, *Palpomyia,* and *Bezzia* groups were fewer in number than most other forms. The *Tendipes militaris* group is rarest, having been taken at only one station on one occasion. The two species of Culicidae recorded were probably victims of surface-water run off from an adjacent swamp, as these are characteristic of stagnant water. The empidids *Hemerodromia* and *Roederiodes,* which were taken only at the swift-water station (station 2), are typically swift-water forms in North America although species of the former have been reported from stagnant water in Europe (Bischoff *in* Johannsen 1935). The stratiomyid *Odontomyia* is generally found in still waters but in this study they have been repeatedly taken from logs in fairly swift waters at station 2. They are, however, more common at downstream stations where the current velocity is less. The ephydrid *Ephydra* sp. belongs to the same genus as the well-known brine fly that occurs in Great Salt Lake. The species present in Homosassa, however, is probably *E. subopaca* which, although a brackish-water form and found in salt concentrations up to 11 $^{0}/_{00}$ (Johannsen 1935), is not present in Great Salt Lake. In Homosassa it was found in salt concentrations of over 8 $^{0}/_{00}$.

EPHEMEROPTERA. The mayflies are represented in Homosassa by seven species, five of which occur in numbers large enough for comparison of their populations (see Fig. 10). *Callibaetis pretiosus* occurs only at station 2 and in very small numbers while *Baetis intercalaris* was taken rarely and only at station 3. *Callibaetis floridanus* is the most widely distributed and abundant mayfly in Homosassa Springs. Its range extends far into the high-chloride waters of the estuary but the numbers of individuals are small in this area. The occurrence of this species in brackish water has been reported by Berner (1950) and Berner and Sloan (1954). *Baetis spinosus* is found at stations 1, 2, 4, and 5 but only in abundance at station 2, the swift-water station. It was rarely taken at slow-water stations although it commonly occurs in quiet water elsewhere (Berner 1950). The distribution of *Tricorythodes albilineatus* is similar to that of *B. spinosus* but the number of individuals collected was considerably smaller. *Cloeon rubropictum* has somewhat the same pattern of distribution as does *T. albilineatus* except that the peak of the density curve of the former is at station 3 instead of 2. *Caenis diminuta,* although present at all stations except 7 and 8, is found in greatest number at station 4. It is apparently fairly tolerant as a species although its populations are seen to be quite small in areas of environmental extremes such as the pool and estuary.

Many species of this order are very sensitive to low concentrations of dissolved oxygen, and for this reason they are sometimes used as indicators of "clean water" (waters of relatively high dissolved oxygen concentrations).

TRICHOPTERA. The Hydroptilidae are the most widely distributed family of the caddisflies with the Leptoceridae being next. Because of the case building habits of this group and the resulting difficulty of collecting quantitatively by the method employed for other insects, little has been learned of the relative abundance of the various species. Like the mayflies, the Trichoptera are generally found in waters which are well aerated; they, too, are sometimes used as "clean water" indicators. The presence of nine species of this insect in the pool at Homosassa out of a total of ten found in the entire river seems to indicate that the dissolved oxygen concentration in the springhead is probably not seriously limiting to this order.

HEMIPTERA. Unlike the other groups of aquatic insects (with the exception of the Coleoptera), the Hemiptera are able to range for considerable distances and are not dependent upon dissolved oxygen. Since nearly all of the Hemiptera are predaceous and their food for the most part consists of aquatic and terrestrial insects and entomostraca, they are found in greatest number, as might be expected, where the concentration of other insects is greatest; that is at stations 2 and 3. *Mesovelia mulsanti* is the most widely distributed species, being found from station 2 to 8. The others have a rather spotty distribution but this is probably due as much to insufficient sampling because of the extreme mobility of these insects as to actual difference in distribution. One form, *Metrobates hesperius ocalensis,* was formerly known only from the Rainbow River in Marion County (Herring 1950). Only four species have been taken in the pool and this may be a reflection of the small numbers of other insects in this area.

COLEOPTERA. Five species of Coleoptera have been collected. All of these are present at station 2; four of them exclusively. Beetles are very few in number and on several collecting trips were not recorded.

LEPIDOPTERA. There are two genera of aquatic Lepidoptera, *Nymphula* and *Elophila,* both of which occur in Homosassa. They are very rarely taken, however, and then at stations 1 and 2 only. Since this order is so poorly represented, it is not included in the frequency histogram (Fig. 9).

ODONATA. The Anisoptera are sparsely distributed in the river. The greatest number of species are found at stations 2 and 1 where the bottom is for the most part firm and free from hydrogen sulfide such as occurs in the substrate of the downstream stations.

The Zygoptera are rather few in number of species but some of these are represented by fairly large populations at certain stations. *Argia sedula* and *A. fumipennis* are the only species limited to the upper region of the run; they are taken but rarely. Others are well distributed in the river as can be seen in Figure 11. This figure also shows the relative sizes of nymphal populations of the Zygoptera. *Enallagma cardenium* is limited to the first four stations and is more frequently taken in the pool than the other species. It attains its maximum abundance at station 2, the swift-water station. *Ischnura ramburii* is more common at station 4 but is completely absent only at station 8. Its presence in waters of high salinities was noted by Pearse (1934) and Wright (1943). *Enallagma pollutum* has the same range as *I. ramburii* (stations 1 through 7) but is much more evenly distributed numerically. It, too, is tolerant of fairly high chlorinities although no reference to this effect has been found in the literature. In fact, Wright (1943) indicates that *E. pollutum* is characteristic of strictly fresh water. *Enallagma durum* has perhaps the most interesting distribution among the damselflies. It is present at all stations except 1 and 2, but is found in greatest numbers in the estuary where the other species are either absent or represented by only a few individuals. Wright (1943) mentions that in the marshes of the Central Gulf Coast, this species reaches its greatest abundance in brackish water. *E. durum* was the only damselfly nymph found at station 8 but here it is present in very small numbers.

WEEKIWACHEE SPRINGS

DIPTERA. The distribution of the Diptera in Weekiwachee Springs is remarkably similar to that in Homosassa; the chief differences being in the near elimination of slow-water forms such as *Odontomyia* and *Ephydra* and the increase in swift-water forms. More species are found in the estuary than is the case in Homosassa.

EPHEMEROPTERA. Only two species of mayflies, *Callibaetis floridanus* and *Caenis diminuta* occur in the pool where the concentration of dissolved oxygen is always low (maximum recorded, 2.5 ppm). *C. floridanus* reaches greatest abundance in the pool and estuary; these are perhaps the two most extreme stations, with respect to environmental factors, in the entire river. The presence of *Callibaetis* in numbers in waters poor in dissolved oxygen is interesting because Gaufin and Tarzwell (1952) recorded no other mayfly but *Callibaetis* sp. from the recovery zone of a polluted stream (min. dissolved oxygen conc., 1.6 ppm), and Dr. F. P. Ide (personal communication) reports two species of *Callibaetis* as being more tolerant than other mayfly forms in a polluted stream in Ontario. The paucity of *C. floridanus* in the stations of the run can probably be accounted for by the fact that this species is primarily a slow to stagnant-water form and the swift current of the run is therefore limiting.

At the station below the boil (station 2), the number of species increases to twelve. From this point on, there is a gradual decrease in species number until at the estuary station only *C. floridanus* is found. *Baetis spinosus* is present in fairly large numbers at stations 3 and 4 but is completely absent at stations 1 and 6. *Tricorythodes albilineatus,* being a swift-water form, is present at all of the swift-water stations in roughly the same numbers but is absent at stations 1 and 6. *Caenis diminuta* is present at station 1 but is found here only in small numbers. A very few specimens were taken at station 2. This is typically a still-water species and its absence from the run is not surprising. *Pseudocloeon parvulum* is found in greatest numbers in the lower regions of the run. It does not occur at station 1 and is found only in small numbers in the middle section of the run.

The peaks of the population curves for the mayflies of Weekiwachee are somewhat different than for Homosassa, partly because of the swift current of the former.

TRICHOPTERA. Only one species of caddisfly, *Leptocella* sp. A, is found in the pool of Weekiwachee Springs as contrasted with nine in Homosassa. The distribution of this order in Weekiwachee is very similar to that of the mayflies except that the greatest number of species of Trichoptera are found at station 3 instead of 2 as for mayflies. The similar distribution of the two groups, at least in the pools, may be due to the generally high oxygen requirements of both. Two species, *Leptocella* sp. A and *Oecetis cinerescens,* persist in the high chloride waters of the estuary. Their absence in the lower Homosassa stations is therefore probably due to some factor other than chloride concentration. The increase in species number over Homosassa may be explained by the presence of more rheophilic forms. There seems to be little difference in numbers of individuals of the same species in the two rivers.

HEMIPTERA. The water striders are more sparsely distributed in this river than in Homosassa. Only one species has been taken in the pool; this, again, may reflect the low level of available food in the springhead area. As in Homosassa, there is a sudden increase in species number below the boil area. It is interesting to note that one form, *Metrobates hesperius depilatus,* is known only from the Weekiwachee River and Salt Creek, a stream which flows into the estuary of Weekiwachee (Herring 1950). This subspecies occurs at all stations but the last. Only *Hydrometra australis* was collected in the estuary.

COLEOPTERA. As in Homosassa, this order is represented by only a few species and by small populations. It is as difficult to explain the paucity of beetles here as in Homosassa. None was taken in the pool, possibly for the same reason as was suggested for the Hemiptera. Three species were found at station 2, five at station 3 and two at station 4. Below this point, none was collected.

LEPIDOPTERA. Both of the aquatic genera are present but not at the same stations. *Elophila* is found only at stations 2 and 3 while *Nymphula* was taken only from stations 4 and 5. As in Homosassa, the numbers of individuals are small in all habitats where these insects occur.

ODONATA. More species of the Odonata, both Anisoptera and Zygoptera, occur in Weekiwachee than in Homosassa. The presence of more dragonfly nymphs may be because the swift current prevents accumulation of large amounts of organic detritus on the bottom of Weekiwachee resulting in less hydrogen sulfide in the substrate. The increase in damselfly nymphs over the number found at Homosassa is difficult to explain as these insects are more often found in waters of less current velocity than that found in Weekiwachee. The number of species in the boil area is the same as for Homosassa; these species are, for the most part, also the same. The low dissolved oxygen in the pool of Weekiwachee is obviously not a limiting factor to these forms. The number of species is greatest at station 3, and then subsides until, in the estuary, only *Enallagma durum* and *Ischnura ramburii* are found. As has been reported by Wright (1943), both of these species are tolerant of brackish water. These forms were also found in the Homosassa estuary along with *Enallagma pollutum.* As may be seen in Figure 13, the observed population densities of the species of Zygoptera are greater in Homosassa than in Weekiwachee Springs.

Statistical Treatment of Quantitative Data

In order to show that the differences in numbers of individuals obtained at the different stations were real and not a result of sampling error, a statistical treatment, analysis of variance, was applied to data obtained from quantitative sampling. The standardized sampling method was as follows: five or more areas were picked at random at a given station. Within each of these areas a five-sweep sample was made (five sweeps has been shown to be an adequate sample; see Fig. 2) and the insects from each of these samples were kept separate. The specimens were later counted and the numbers compared statistically with those of collections made (1) at different times but at the same stations, (2) at different times and at different stations, and (3) near the same times but at different stations. The results of these analyses substantiated the conclusion that population density gradients exist in the runs of both rivers. For example, numbers of individuals in samples taken from H-1 were significantly (*P* less than .01) less than those from H-2 and from H-3, both in April and in November. Numbers were not significantly different (*P*. greater than .05) in samples taken at H-1 at different seasons (April and November). The same was true for samples taken from W-1 at different times. Numbers were, however, significantly lower at W-1 than at W-2 or at W-3. Significant differences were shown to exist between numbers present in samples taken from H-3 in April and in November. The greater seasonal fluctuation in temperature at station H-3 may, in part, account for this observed seasonal variation in density while the more constant temperatures at W-1 and H-1 are probably instrumental in compressing population density fluctuation in these areas.

DISCUSSION

The two major features that are similar in both Homosassa and Weekiwachee Springs are temperature and pH (see Tables III, IV). Dissolved oxygen (Figs. 3, 5) and chloride concentrations (Figs. 4, 6) differ considerably in the springheads of the two springs. Dissolved oxygen concentrations are essentially the same in the lower halves of both rivers but chloride concentrations are alike only in the estuaries. The only point in Homosassa at which the current velocity is somewhat comparable to that of Weekiwachee is at station 2. Another condition which is no doubt common to both springs, at least in the springhead areas, is a limited number of ecological niches. Because of the nearly constant conditions which exist in these areas, available niches should be relatively few in both (H. T. Odum *in* E. P. Odum 1953, p. 251).

By referring to Figures 7, 8, and 9, it can be seen that the general trend in both rivers is for species numbers to be initially low at the pool, to increase rather sharply at the next one or two stations below the springhead, and then gradually to decline as the estuary is approached. In the freshwater sections of both rivers there is a striking correlation between this distribution and dissolved oxygen concentrations. Since experimental evidence concerning the oxygen requirements of the species in question is lacking, the existence of a real relationship must remain speculative until such evidence is forthcoming. However, many observations regarding the paucity of related species in waters of low dissolved oxygen concentrations seems to suggest that, at least in the springhead areas, this may be an important limiting factor. (Campbell 1939; Gaufin and Tarzwell 1952).

The phenomenon of species number reduction in boil areas is more obvious in Weekiwachee (Fig. 8) than in Homosassa Springs (Fig. 7). Since the dissolved oxygen concentration is considerably higher in the pool of Homosassa while many other factors are common to both pools, this would seem to lend weight to the suggestion that dissolved oxygen concentrations of these magnitudes are insufficient for some species. There is a complicating factor, however, which cannot be ignored. That is that small fish (primary carnivores) are commonly observed in the springhead of Weekiwachee Springs but are only rarely seen in this area of Homosassa where the larger fish (secondary carnivores) presumably prevent their establishment. Predation pressure by the small fish in Weekiwachee may have the effect of eliminating those insect species whose eggs and larvae or nymphs are most easily seen and captured.

In the mid-sections of both rivers conditions are not nearly so invariable as near the sources. This variability is shown in part by the dissolved oxygen fluctuations in the downstream areas (Figs. 3, 5) and by slight but significant temperature fluctuations in these sections (Table IV). It seems reasonable that the increased number of ecological niches provided by this variety could result in establishment of larger numbers of species in these areas. Conversely, the limitation of species in springheads is possibly in part due to the nearly constant environmental conditions found there. This may serve to limit all but those species whose developmental optima fall within these narrow limits of variation.

The reduction in species numbers as the estuaries are approached is almost as striking as the similar phenomenon at the sources. There is good agreement between this reduction and the increase in chloride concentration. Here again, however, experimental evidence regarding chloride tolerances of the species under consideration is meager. Pearse (1934) made observations on insect distribution in brackish-water pools at Dry Tortugas. He found *Microvelia borealis, Trichocorixa sellaris,* and larvae of *Chironomus* sp. in a pool whose salinity range was recorded as 20.30 to 73.32 $^0/_{00}$ (11.2 to 40.6 $^0/_{00}$ chlorinity) through the summer months. *Ischnura ramburii,* which in the present study was found in waters of approximately 4.5 $^0/_{00}$ chlorinity, was taken by Pearse from pools in which the recorded salinity range was 19.38 to 23.65 $^0/_{00}$ (10 to 13.1 $^0/_{00}$ chlorinity). Osburn (1906) found that *I. verticalis* could survive (for an undisclosed period) in sea water whose density was 1.01 at 72 F. (chlorinity approximately 8 $^0/_{00}$) but died within a day or two when placed in sea water of density 1.015 (chlorinity approximately 11 $^0/_{00}$).

These data are pitifully few but they indicate that at least two of the species recorded from the Florida springs, along with several related species, can tolerate chlorinities considerably in excess of those in the estuaries of the two rivers. One possibly important difference in these studies is that Pearse and Osburn worked in ponds whose salinities were not subject to tidal fluctuation. The species that are found in the lower stations of the Homosassa and Weekiwachee estuaries must, however, withstand daily chloride fluctuations of 1 to 5 parts per thousand. Although the osmotic stress is not so great as in fresh or sea water, the insect still must solve the problem of periodic fluctuation and differing ion ratios from that of its body fluid (Buck *in* Roeder 1953). This is perhaps as important a barrier as concentration itself. Other factors, such as decreases in the amounts of vegetation (and thus a decrease in protected areas) and changes in the nature of the substrate, are probably contributory to the formation of distribution patterns in the lower reaches of both rivers.

For those species whose densities were quantitatively compared (Figs. 10-13) the frequency disstribution was found to follow roughly the same pattern as the species distribution. That is, small populations in the springheads, increasing numbers downstream, and reduction again as the estuaries are approached. The latter phenomenon is partly a result of the elimination of many groups, presumably by the high chloride concentrations and fluctuations of the estuaries. The population peaks of a few species, such as *Enallagma durum,* are in the higher chloride ranges but these, too, soon decline. In the estuary of Weekiwachee Springs, *E. durum* and the mayfly *Callibaetis floridanus* reach the peak of their densities at chloride concentrations which approach 5.5 $^0/_{00}$ at high tide. The chloride fluctuation due to tide in this area is about 5 $^0/_{00}$.

Because of the presence of small fish in the pool of Weekiwachee, as was discussed above, fish predation may be instrumental in keeping the numbers of insects depressed. This cannot explain, however, the correspondingly small numbers of individuals found in the Homosassa pool. In Florida springs in general, planktonic forms are practically absent in boil areas. The lack of this important food source should certainly limit the numbers of individuals of those species which are dependent, either primarily or secondarily, on such a food source. But it is difficult to understand how this could affect those species, such as some mayflies, which feed on the epidermis and epiphytic algae of higher plants.

The question of species being restricted to certain plants as a factor explaining distribution should be mentioned. Although it is known that a few species of aquatic insects are limited to one or a few host plants, this condition is far less common than among terrestrial species. McGaha (1952) reports that even though some emergent plants may shelter restricted insect species, those species which inhabit totally submerged plants show practically no specificity. Even species frequenting emergent plants have a wide range of food plants (Frohne 1938). In the present study no restricted plant-insect species associations were noted although it must be admitted that this aspect was not given detailed consideration.

There are certain similarities between the fauna of the pools of the two springs studied and that of organically polluted water. Some forms, such as blood worms (*Tendipes*) and the mayfly nymph *Callibaetis*, which are known to be tolerant of varying degrees of organic pollution, are found in springheads. On the other hand, forms such as most of the other mayfly species and caddisflies, which are sometimes used by sanitation biologists as "clean water" indicators (Claassen 1932; Campbell 1939), are notably few, especially in the pool of Weekiwachee. These data do not, of course, suggest that the springheads are at all polluted but perhaps only that one of the major results of organic pollution, low concentrations of dissolved oxygen, is common to both situations.

The chemical constancy of springheads has been demonstrated by dissolved oxygen determinations and pH and temperature measurements during this study and by many chemical analyses made by the Florida Geological Survey over a period of several years. Evidence that insect population sizes do not change significantly in these pools with the seasons was presented in the section on statistical treatment. Thus the nearly constant environmental conditions seem to be reflected in the constant sizes of populations found in these areas.

Summary

Two constant-temperature Florida springs, Homosassa and Weekiwachee Springs, have been studied and an attempt has been made to correlate the spatial and temporal distribution of aquatic insects with measured physical and chemical environmental factors. This investigation was conducted from November 1952 to February 1954. The major results of the study may be briefly summarized as follows:

1. The dissolved oxygen concentrations form gradients in both springs but this is more pronounced in Weekiwachee than in Homosassa. The dissolved oxygen content is typically lowest in the springhead areas but increases fairly rapidly with distance down the runs.

2. In the lower parts of the runs, the chloride concentration increases due to the effect of marine tidal invasion. The chloride content in Homosassa Springs begins in the oligohaline range and the concentration becomes gradually greater in the estuary. In Weekiwachee Springs, however, the chloride concentration is low and never reaches the oligohaline range in the run. The change from fresh to brackish water is very abrupt in the estuary.

3. Temperature was found to be essentially constant in the springheads of both rivers; the daily and seasonal changes in temperature at downstream stations, even those several miles below the pools, were not of large magnitudes.

4. The pH is nearly constant in the springheads and runs but varies somewhat in the estuaries; this is probably due to changes in the salt concentrations during tidal inflow and outflow.

5. By using as indices dissolved oxygen fluctuation and temperature variation, areas of environmental variability were found to lie at points considerably below the springheads.

6. Gradients of both numbers of species and densities of populations exist in both rivers. The numbers of species and individuals are fewer in springhead and estuarine areas than in mid-sections of the rivers. This is statistically verified. Factors which may in part explain the observed distribution patterns are discussed.

7. The similarities between certain of the fauna of springhead areas and that of organically polluted waters is pointed out. This may be accounted for by the fact that in both situations dissolved oxygen concentrations are low.

8. Evidence is presented which indicates that, at least with respect to insect populations, springheads are areas of biological as well as chemical constancy.

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ECOLOGICAL ASPECTS OF THE SYMPATRIC DISTRIBUTION OF MEADOWLARKS IN THE NORTH-CENTRAL STATES[1]

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Students of avian distribution have long been intrigued with the sympatric relationship of the two species of meadowlarks in the central region of the United States.[2] The eastern meadowlark (*Sturnella m. magna*) and the western meadowlark (*Sturnella n. neglecta*) have overlapping breeding ranges extending from Oklahoma northward into southern Ontario. This paper is the report of a study of historical and ecological aspects of this sympatric distribution and proposes an hypothesis to explain the distributional changes that have occurred within recent years. The equally intriguing relationship between *S. n. neglecta* and other races of *S. magna,* south of Oklahoma, will be omitted from the present discussion due to the paucity and conflicting nature of the reports from that area.

I am greatly indebted to numerous amateur and professional ornithologists who have contributed distributional data for this analysis, and I regret that lack of space permits only a listing of their names in an appendix at the end of the paper. I am especially grateful to the following individuals who have given generously of their time to various aspects of the study: Mr. Vincent Batha, Mrs. A. J. Binsfeld, Mr. and Mrs. George Crossley, Miss Doris Gates, Mr. and Mrs. Kenneth Krumm, Mr. Philip Mallow, Mr. Thomas Morrissey, Miss Margarette Morse, Mr. Russell Mumford, Mr. Alvin Peterson, and Mr. and Mrs. George Spidel. Special thanks are due to Dr. John T. Emlen, Jr., Department of Zoology, University of Wisconsin, for his contribution to the study and assistance in preparation of the manuscript. For a critical reading of the manuscript I would like to express thanks to Dr. John T. Curtis of the University of Wisconsin, Dr. Ernst Mayr of Harvard University, and Dr. Harrison B. Tordoff of the University of Kansas.

Former Distribution

Early records of meadowlark distribution are inadequate for a detailed account of progressive changes. As an alternative all available records made before 1900 have been pooled to provide an approximate picture of the breeding ranges of the two species at the turn of the century. The range maps are based in part on published material and in part on extensive personal communication with current workers in strategic localities. Because of the many irregularities of distribution and reporting techniques, it seemed desirable to present the ranges in a generalized form. Those readers who are interested in the details of local distribution should refer to the original sources of documentation as listed in the appendix.

The approximate limits of the critical zone of overlapping breeding ranges of eastern and western meadowlarks, at the turn of the century, are indicated in Map 1. The eastern species could be found breeding regularly and commonly throughout most of the area east of line E. In addition it was recorded as present in isolated, peripheral colonies beyond this region in the limited area indicated by the horizontal lines extending westward from line E (zone 1). The western meadowlark could be found breeding regularly and commonly throughout most of the area west of line W. It in turn was recorded as breeding in isolated, peripheral colonies beyond that region, as indicated by the horizontal lines extending eastward from line W (zone 3). Particular attention is called to the narrowness of the zone throughout which both species were formerly found as regular, contiguous breeders (zone 2 in Map 1).

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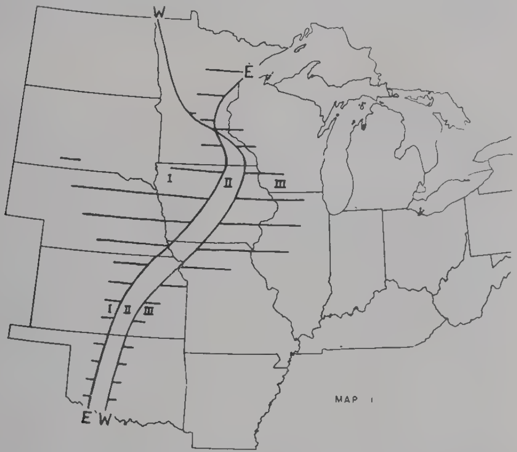
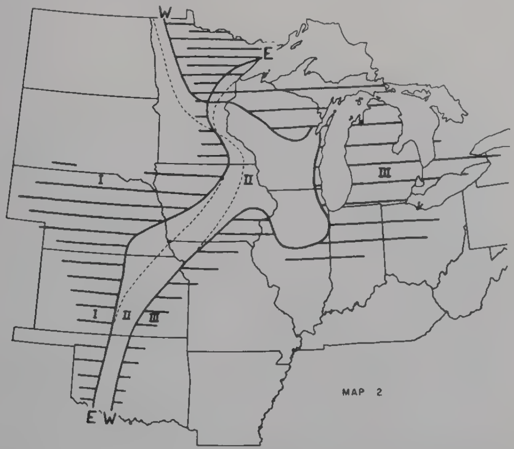
[1] This research was supported by funds from the Wisconsin Alumni Research Foundation and represents one phase of a four year study of comparative meadowlark ethology and ecology conducted at the University of Wisconsin.

[2] The taxonomic relationship of these species is, in itself, an interesting problem and in some contention among contemporary ornithologists. Though this aspect will not be treated here, the author is convinced, by virtue of his own research, of the wisdom of their recognition as full species. It is with that understanding and interpretation that this paper is presented.

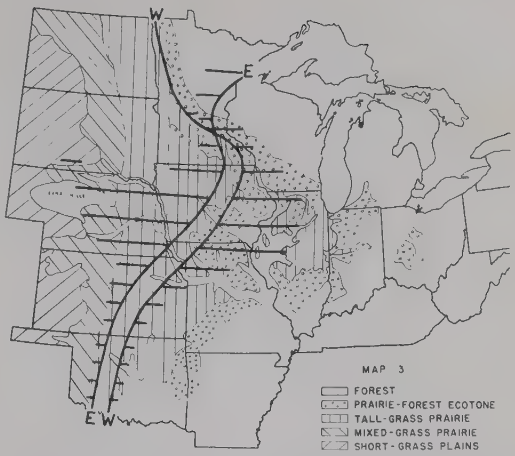


Map. 1. Region of overlapping breeding ranges in 1900. Zone I—Isolated colonies of eastern meadowlarks. Zone II—Area where both species bred commonly. Zone III—Isolated colonies of western meadowlarks.

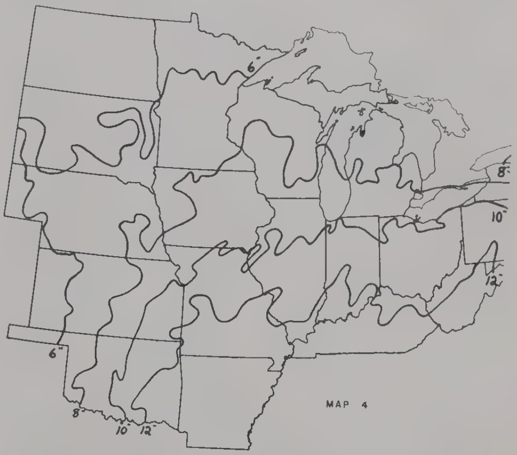


Map. 2. Region of overlapping breeding ranges in 1950. Zones as in Map 1. Dotted lines indicate former boundaries of Zone II.

From an ecological standpoint the "former breeding ranges" of these species are more significant when superimposed upon a map of the original vegetation of the north-central states, as in Map 3.



Map. 3. Relationship of "former breeding ranges" with original vegetation (adapted from Carpenter 1940, Ecol. Monog. 10).



Map. 4. Average spring precipitation, March thru May. (Adapted from USDA Yearbook 1941.)

Carpenter's (1940) map of the grassland biome gives in a general way the original extent of short-grass plains, mixed-grass prairie, tall-grass prairie, and the prairie-forest ecotone. The region to the east of these zones was largely forested.

There are obvious limitations in interpreting the relationship between meadowlark ranges as of 1900 with the undisturbed, native vegetation. In spite of the inadequacy of such a comparison, some interesting points are suggested. There appears to have been a correlation, regionally at least, between the former breeding ranges and original vegetation, in that the western meadowlark occurred eastward to the forest edge and the eastern meadowlark could be found westward to the prairie. A notable exception to this general correlation can be seen in the south where, as of 1900, the western species had failed to colonize much of the tall-grass prairie of Oklahoma, Kansas and Missouri, and the eastern species had penetrated well into the prairies of those states. The absence of the western bird in this region is more striking in light of its subsequent invasion of forested areas to the northeast.

Current Distribution

The changes that have taken place in these overlapping breeding ranges during the past fifty years have been well-documented and are indicated in Map 2. Of the two species, the eastern meadowlark has exhibited a more stable breeding range during this period than the western bird. While there has apparently been an increase in the number of its localized breeding colonies at the range periphery, the eastern species has invaded very little new territory. The range expansion of the western meadowlark, on the other hand, has been rather extensive.

This eastward spread of the western meadowlark has been limited to the northern half of the area under discussion. No major eastward advance of the western species has been noted in Oklahoma, Kansas or Missouri during the past fifty years, yet observers in Wisconsin have seen it arrive and watched it increase to a point where it now outnumbers the eastern bird in many southern counties (Lanyon 1953). In Michigan the western species, almost unknown until the 1930's, can now be found breeding in pioneer colonies in nearly all counties of the State.

There has been, then, a marked stability of the breeding ranges of both species in the southern half of the region under discussion, the zone of overlap there having remained relatively narrow for as long as we have ornithological records. The tendency toward a broader zone of overlap toward the north, as indicated by the presence of peripheral colonies in 1900, became more fully expressed in the last fifty years, largely as a result of the eastward surge of the western species.

Differential Habitat Preference

The region of current overlap of these breeding ranges (Map 2) is an extensive one. In view of this, current evolutionary theory presupposes that a certain degree of ecological divergence must exist between these two closely related species, if they are to continue to occupy the same geographic region. In order to investigate this aspect of their sympatric relationship, I assembled the information that was available in the literature concerning habitat selection in these species and added personal observations as well as those of other workers in various parts of the region of overlap. For purposes of simplifying the presentation, the data will be considered with respect to the three zones indicated on the range maps: (1) The western zone, where the western species is dominant and the eastern meadowlark is restricted to isolated breeding colonies; (2) the central zone, in which both species breed in good numbers and in a matrix of contiguous populations; and (3) the eastern zone, where the eastern species is dominant and the western meadowlark is found only in isolated breeding colonies.

Zone 1

It is the western meadowlark that is heard almost exclusively throughout western Oklahoma, Kansas and Nebraska, yet the eastern species is known to occur there in localized breeding colonies. Tordoff (1953: in litt.) called my attention to such a colony of eastern birds in southwest Kansas, located in a lowland area of comparatively lush vegetation and natural springs (Fig. 1). Oberholser and McAtee (1920) recognized an affinity of the eastern meadowlark for the "valley meadows" of western Nebraska, and Youngworth (1953: in litt.) and Benckeser (1953: in litt.) have cited a similar differential habitat preference in this region.

In traveling through the sand-hills of Nebraska, where one hears only the western meadowlark on the extremely dry uplands, I was intrigued by the presence of eastern meadowlarks in a number of "pockets" of moist lowland, where scarcely a tree was in sight (Fig. 2). Still further north, in southwest South Dakota, this same ecological relationship has been described from an early date by Tullsen (1911) and more recently by Krumm (1953). Larson (1925), reporting from south-

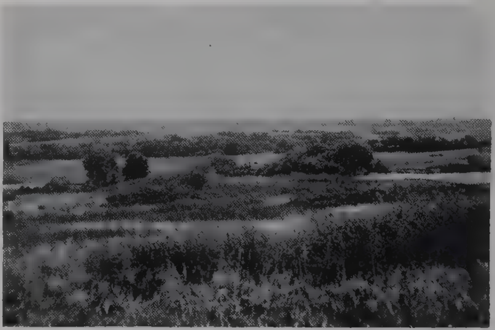


Fig. 1. Site of an isolated colony of eastern meadowlarks in Barber County, southwest Kansas (May 1954).

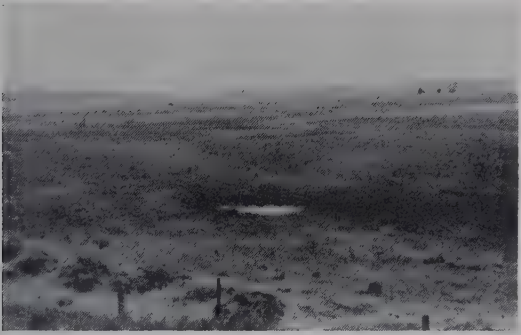


FIG. 2. Site of an isolated colony of eastern meadowlarks in Cherry County, northwest Nebraska (May 1954).

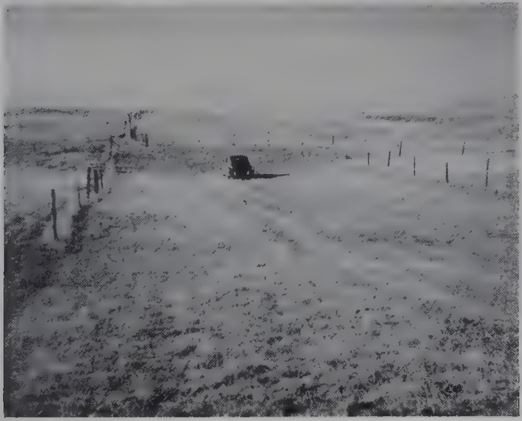


FIG. 3. The rolling plains of Lincoln County, western Nebraska, support large numbers of the western species but no eastern meadowlarks (photo by Miss Doris Gates, April 1953).

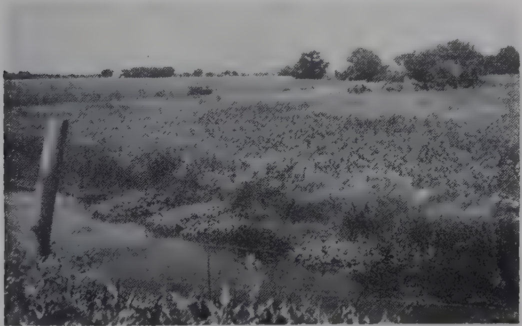


FIG. 4. Isolated colonies of eastern meadowlarks occur on the wet meadows along the Platte River, as here in Lincoln County, western Nebraska (photo by Miss Doris Gates, July 1954).

eastern South Dakota, considered the western species "more of a bird of the uplands," while the rare eastern bird was "more likely to be found along the river bottom and the lower valleys."

In Lincoln County, western Nebraska, Gates (1953: in litt.) conducted a standardized "singing-male, roadside census"[3] of meadowlarks over an area of 200 square miles (Fig. 3). Only four per cent of a sample of 1134 meadowlarks were the eastern species, all of which were found on the wet lowlands along the Platte River (Fig. 4).

Though the western meadowlark is present in greatest numbers on the open plains of zone 1, it may also be found in the moist lowlands where it has presumably been forced by intense intraspecific competition. In western Nebraska, for example, one may observe both the western meadowlark and the sora rail without shifting the field glass, whereas this relationship would be unlikely in zone 2 and highly improbable in zone 3.

Zone 2

In central Oklahoma, where both species occur in numbers, Baumgartner (1951: in litt.) has suggested that the western meadowlark may be better adapted to the short and mixed-grass pastures whereas the eastern species may find more favorable conditions in the tall-grass prairies. Although both species occupy the wheat fields and pastures of east-central Kansas, Tordoff (1953: in litt.) has noticed an affinity of the eastern birds for smaller fields, deeper vegetation and damper soils, whereas the western birds show a preference for the larger fields, shorter vegetation and better drainage.

In southeast Nebraska, the Spidels (1953: in litt.) conducted a standardized census of the meadowlarks over an area of 140 square miles. With their sample of 359 meadowlarks, of which 19% were the eastern species, it is possible to demonstrate a statistically significant correlation between distribution and elevation, the eastern species being more common on the lowlands and the western species being more common on the uplands. The independent observations of Glandon (1948) and Whelan (1940) indicate a similar differential habitat preference in this region of Nebraska.

Further standardized censuses conducted in central Iowa by Binsfeld (1953: in litt.), and in northeast Iowa by the Crossleys (1953: in litt.), show a similar correlation of the distribution of these species with elevation. Stewart (1953: in litt.) has also observed this in northeast Iowa and remarked in particular about the apparent preference of the western species for the drier habitat. In southeast Minnesota, Warner (1950) found both species present but "each was found to be quite distinct from the other in its choice of habitat. The eastern was restricted to the valley while the western was found only in the uplands."

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[3] This was thought to be the most efficient method of providing an index of the relative distribution of these species over a large area, and has been the technique utilized by all of the cooperators in this study. Briefly, the procedure consisted of counting the number of singing males of each species that could be heard in one minute periods, over a grid of stations spaced at approximately one-mile intervals. This provided a random sample of the breeding populations of the area, regardless of land cover or topography.

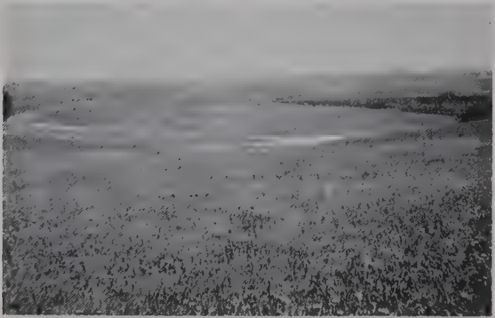

FIG 5. The "uplands" of southern Wisconsin, originally covered with tall-grass prairie, now support the largest concentration of western meadowlarks in that State (May 1954).

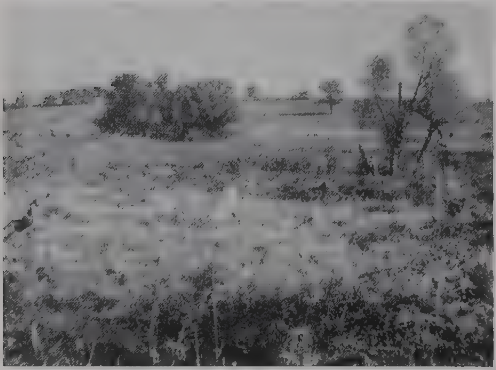

FIG. 6. Lowland meadows and wooded pastures support the largest number of eastern meadowlarks in southern Wisconsin (August 1953).

In southern Wisconsin, now well within this central zone, an intensive census was made of the meadowlark population throughout an area of 1300 square miles. With the assistance of Emlen, Batha, and Mallow, a sample of over 2500 meadowlarks was accumulated. The results of this work (MS in preparation) corroborate the findings and observations mentioned for the other states included in this central zone. A statistically significant correlation was found to exist between the distribution of the meadowlark sample and the elevation of the area censused (probabilty of χ^2 less than .01). In this area of southern Wisconsin, the upland regions support the largest population of western meadowlarks, whereas the lowlands (stream valleys and marshy or poorly drained regions) support the heaviest concentration of eastern meadowlarks (Figs. 5, 6).

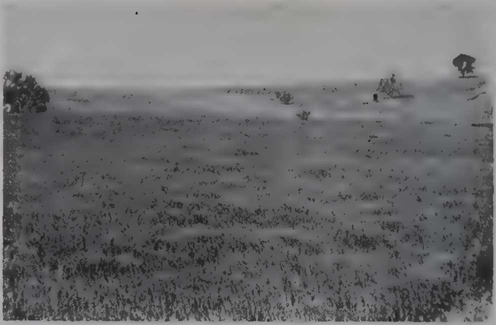

FIG. 7. Site of an isolated colony of western meadowlarks in Gentry County, northwest Missouri (May 1954).

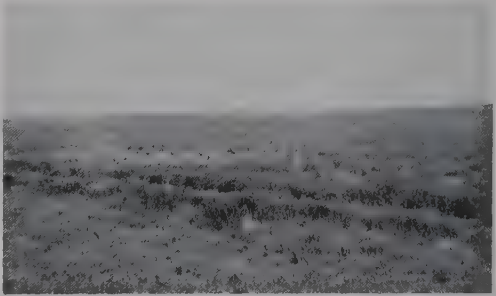

FIG. 8. Sandy river terraces, as this one along the Mississippi River in Illinois, have often been the site of pioneer western meadowlark colonies (May 1954).

The "uplands" represent some of the more subhumid climate communities available in southern Wisconsin. Originally they were covered with two types of prairie, (1) high prairie and (2) dry lime prairie (Curtis and Greene 1949), both characterized by well-drained soil that may become very dry during the summer.

Curtis and Greene also differentiate a third type of prairie, the sand prairie, in Wisconsin. Sand prairies are located on residual sands in the Driftless Area, in glacial lake beds, and on river terraces of glacial outwash. A number of observers have reported concentrations of western meadowlarks on the sand prairies in the Wisconsin and Mississippi River valleys. Peterson (1953: in litt.) conducted a standardized census of meadowlarks over a 140 square mile area located near the mouth of the Black River. Originally there were extensive sand prairies located in this portion of the Mississippi valley. Beyond the palisades to the east are the stream valleys and formerly well-timbered bluffs. At 83 listening stations located on the prairie area, Peterson recorded 134 western birds, while the sample from 52 stations located in the valleys and on the bluffs to the east contained only 7 western birds.

A possible exception to this correlation of meadowlark distribution with environmental moisture has been reported by the Hamerstroms (1953: in litt.) at Plainfield, Wisconsin. There the western meadowlark is reported to be most abundant on the peat soil of the large, open farmland, while the eastern species is found in greatest numbers on the sandy soil of the smaller, more wooded farms.

Zone 3

Observations of pioneering western meadowlarks at their eastern range periphery afford the best indicator of what constitutes optimum habitat for the species, just as we looked to zone 1 for this information in the case of the eastern species.

Observers in northern Wisconsin, throughout Michigan, and southern Ontario have had difficulty in detecting an affinity of their isolated western birds for any particular habitat. This can be attributed, in part at least, to the greater uniformity of topography and land cover throughout this region than elsewhere in the area under discussion.

In northwestern Missouri I found peripheral colonies of western meadowlarks on the upland ridges of prairie, surrounded by eastern birds that were to be found in many habitats (Fig. 7). Occasionally the localities selected by pioneering western meadowlarks further north in zone 3 will appear suggestive of the species' main range to the west. A large tract of land in northwest Indiana, for example, has been the site of a colony of western meadowlarks for at least the past decade; it lies within the prairie peninsula and still retains some of the physiognomic aspects of a prairie habitat. At Springfield, Illinois, a male western meadowlark has held a territory for the past three years at the Capitol Airport, and truly represents a peripheral, pioneer bird. It is tempting, indeed, to presume that the "plains" aspect of the closely mowed airport was an important factor in the selection of that particular site.

Reports of the first colonies of the western species that became established in the prairie-forest ecotone of Wisconsin (Lanyon 1953) may be included as evidence here, for this region was formerly representative of zone 3 (see Map 1). Early Wisconsin observers were aware of an "island effect" created by the restriction of western meadowlarks to isolated patches of prairie, surrounded by a "sea" of eastern birds. Evidence of this contagious distribution still remains today in that, in spite of a half-century of population build-up and overflow into surrounding habitat, the western species occurs in greatest numbers on these areas of original grassland in southern and western Wisconsin.

Emlen recently conducted a standardized census of meadowlarks throughout a 216 square mile area in Iowa County, Wisconsin, of which 49 square miles were considered "high prairie" at the time of the original land survey (1833-1834, Original General Land Office Plats, U. S. Dept. of Interior). He found that the western meadowlark averaged 1.91 birds per station throughout the entire census area and 3.28 birds per station on the "prairie." I conducted another census throughout a 216 square mile area in Dane County, Wisconsin, of which only 33 square miles were originally "high prairie." In this sample, the western species averaged 2.01 birds per station throughout the census area and 2.85 birds per station on the "prairie." The correlations in each of these censuses are significant at the 1% level.

Shortly after the turn of the century, Stoddard (1953: in litt.) found the western species just appearing in scattered breeding colonies on the sand prairies of Sauk County, Wisconsin. Likewise, some of the earliest colonies of western meadowlarks in Illinois appeared on the sand prairies along the Illinois River (Vestal 1913; Bellrose 1953: in litt.). At Davenport, Iowa, where the western species is a recent newcomer, Morrissey (1953: in litt.) noted that the western meadowlark first colonized the broad, sandy Mississippi River terraces and from there spread out to other "flat or slightly rolling districts where the soil was sandy and ground cover sparse" (Fig. 8).

Discussion of Limiting Factors

Though the breeding ranges of these species at the turn of the century were correlated in a general way with the original vegetation, certain departures from this correlation have been indicated in the southern portion of the region under discussion. An hypothesis recognizing vegetation as the dominant factor limiting their distribution is untenable in view of the tolerance exhibited by both species for a variety of plant associations. A resident of Wisconsin, familiar with the eastern meadowlark as an inhabitant of small farm clearings and wooded pastures, need only to travel to eastern Kansas and central Oklahoma to find evidence for this adaptability. Here one finds the eastern species an abundant breeding bird on the prairie where scarcely a tree breaks the open landscape. The western meadowlark has recently become established in regions having vegetational characteristics far different from what it was exposed to in the grassland areas to the west. Furthermore, the absence of the western bird on parts of the southern prairie would suggest that some factor other than vegetation is dominant in limiting distribution.

The one factor by which the preferred habitats of the two species are most consistently distinguished, in a given locality within the north-central states, is environmental moisture. Throughout this region of overlapping breeding ranges, the eastern meadowlark exhibits a preference for the more moist areas while the western meadowlark selects the more xeric environments.

Unfortunately there is no single adequate index of environmental moisture for such a large area as that under discussion here, due to varying conditions of seasonal precipitation, wind, solar radiation, and edaphic conditions. In the absence of the desired measurements, the breeding ranges of the two species were studied with reference to rainfall data and were found to show a strong correlation with average spring precipitation (March through May). The pattern exhibited by the isohyets in Map 4 corresponds to the northeast-southwest trend of the zone of overlapping meadowlark ranges in Map 2.

Any discussion of the *modus operandi* of environmental moisture in its limitation of the breeding ranges would be quite speculative at this time. The lack of a correlation between breeding distribution and summer precipitation makes it unlikely that the moisture factor has any direct regulatory action upon the breeding biology. Lack (1944) has minimized the importance of any direct effect of physical factors in the environment in accounting for habitat limitations in birds. The correlation noted between breeding ranges and average spring precipitation suggests that the conditions of the breeding environment, as for example the height and density of the ground cover and the resulting microclimate may be most critically expressed during the period of actual territory selection (the months of March and April in these states).

An hypothesis recognizing environmental moisture as an important factor limiting the distribution of breeding meadowlarks would help to explain the curious absence of one or the other species in otherwise suitable habitat. The eastern meadowlark, for example, has been long-established in the wheat country of eastern Kansas and yet has never invaded the wheat fields of the drier western half of that State. On the other hand, the western meadowlark is only occasionally a summer resident in the more moist region east of the Flint Hills in Kansas, though most of that region was once an expanse of tall grass prairie; nor has the western species ever penetrated eastward or southward from its original pioneer colonies in the extreme northwest corner of Missouri, though the uplands of northern and western Missouri were originally rolling prairies and now constitute one of the major blue grass regions in the country.

Another anomaly in the distribution of the western meadowlark has been the inability of that species, to date at least, to take advantage of more of the rich farmland of the Grand Prairie of central Illinois. Although undisputedly an arm of the great grassland area to the west, much of the Grand Prairie originally differed from the prairies of northern Illinois and southern Wisconsin in being poorly drained, low prairie, frequently covered with standing water during the spring months. According to the environmental moisture hypothesis this would have discouraged colonization by the western species, known elsewhere to favor the more xeric habitats. In recent years this region has been drained and intensively cultivated and it may be that the increase of the western meadowlark in the northern third of Illinois can be attributed in some measure to this creation of a drier breeding habitat.

It is proposed that the availability of suitable habitat has also been operating in the delimitation of meadowlark breeding ranges, in a more or less dual capacity with environmental moisture. The stability of the rather narrow zone of overlap in the south, in a region of a steep rainfall gradient, can be attributed to both species' occupying, at an early date, all suitable habitat within their tolerable limits of environmental moisture. In the north, where the rainfall gradient is much more gradual, the narrowness of the former zone of overlap must have been determined primarily by lack of suitable habitat. With the settlement of the land and resulting artificial creation of great areas of "grassland," a dramatic range expansion occurred, resulting in the sweeping eastward invasion of the western meadowlark, still in progress today. During the course of man's alteration of the landscape and the subsequent readjustment of these breeding ranges, both habitat availability and environmental moisture came into play as limiting factors, with the expansion movement being confined only to the new habitat located within the region of tolerable moisture conditions.

The suitability of the newly created habitat, with regard to factors other than environmental moisture, may conceivably have been involved in the speed with which colonization and population growth occurred. There was apparently a time lag between the settlement of the land, which was well underway by the middle 1800's, and the earliest indication of range expansion of the western species, at the turn of the century. Since Wisconsin has been involved in the greater share of this range expansion it is very likely that the change in agricultural economy that occurred in this State just prior to 1900 may have played a role in controlling the inception and speed of the invasion. Prior to 1880, most of Wisconsin's farmland was devoted to the production of cash grains, mainly wheat. Gradually, however, there was a shift to livestock and dairy farming, accompanied by greatly increased acreages of hay and pasture that would have provided optimum conditions for colonization and subsequent spread of a pre-adapted meadowlark from the west.

Recent investigators (Lack 1949, Svärdson 1949) have made the distinction between proximate and ultimate factors in habitat selection. Such stimuli as environmental moisture or physiognomic aspects of the vegetation would be classified as proximate factors, operative in the immediate selection of a particular type of habitat. It is generally believed that, ultimately, the habitat limits of any species have been determined through natural selection, whereby competition has forced the species into the habitat where it is best adapted to survive. The nature of these adaptive differences are known for very few pairs of sympatric species and, as in most instances, the evidence with regard to the meadowlarks in the north-central states is entirely circumstantial.

ECOLOGICAL REPLACEMENT

Perhaps the most intriguing aspect of the relationship of these species in the north-central states is the possibility that the eastern meadowlark is being replaced in certain localities by the western species. Though there is still a definite need for quantitative measurements to demonstrate the existence and extent of this replacement, the independent observations of a number of observers have suggested that it has occurred, particularly in those areas recently invaded by the western species. Observers in Michigan and northern Indiana, where the western meadowlark has only recently become established in isolated, peripheral colonies, have a unique opportunity to study this phenomenon by means of accurate, year-to-year censuses.

Ecological replacement has been observed or postulated in the study of a great many species-pairs (Lack 1944, Moreau 1948 and Svärdson 1949). In the case of the meadowlarks in the north-central states, it is quite logical that the tremendous changes in land cover, the subsequent northeastward invasion of the western species, the the accompanying changes in balance between inter- and intraspecific competition could have resulted in observable population changes of this nature.

It is generally accepted that these birds achieved their rank of full species as a result of having been isolated during the Pleistocene period and that the zone of contact in the north-central states represents a subsequent meeting of the forms (James 1888; Chapman 1900, 1924; Huxley 1940). We will probably never have the information to date the occurrence of this secondary meeting or to determine how their relative distribution was affected by such changes in land cover as the post-Pleistocene extension of the prairie into the northeast states.

One possible explanation of this secondary meeting is based on the assumption that the two forms were effectively isolated as recently as the time of arrival of the white man on the North American scene. The eastern meadowlark, having followed the westward movement of the agricultural frontier, became the native species over much of Michigan and Wisconsin. In the absence of interspecific competition, its population in these areas grew to a point where it was able to colonize virtually all habitat types, including sub-marginal areas (in terms of environmental moisture). Not long after the frontier had reached the prairie, pioneering western meadowlarks began to invade the newly created habitat to the east. Initially the western bird, pre-adapted for sub-humid conditions, colonized the more xeric habitats. Gradually there was a "linking up" of these isolated colonies and, coupled with a shift in agricultural economy that provided optimum meadowlark habitat, the eastward movement of the western species assumed the proportions of an invasion. Competition for breeding sites must have been unusually keen during this period of readjustment, with the western species replacing the eastern bird in many localities where it was actually better adapted. Without accurate measurements of the comparative rates at which this replacement is occurring, we are at a loss as to how far this phenomenon has proceeded or how much longer it will continue.

SUMMARY

A study has been made of historical and ecological aspects of the sympatric distribution of the

eastern meadowlark (*Sturnella m. magna*) and the western meadowlark (*Sturnella n. neglecta*) in the north-central United States. Maps are presented, indicating the approximate limits of the former breeding ranges and the current breeding ranges for the region under discussion. Though the ranges of both species have remained comparatively stable in the south, there has been a well-documented northeast extension of the range of the western species during the past fifty years.

Field observations and censuses indicate a differential habitat preference in that the preferred habitats of the two species in a given locality are most consistently distinguished by their environmental moisture. The eastern meadowlark exhibits a preference for the more moist areas while the western meadowlark selects the more xeric environments. A correlation between the overlapping breeding ranges and average spring precipitation is further evidence that environmental moisture may be a major proximate factor in limiting meadowlark distribution.

It is proposed that the availability of suitable habitat has also been operating in the delimitation of these breeding ranges, in a dual capacity with environmental moisture. Since both species have exhibited a tolerance for a variety of plant associations, the physiognomic aspects of the vegetation would appear to have only secondary importance in limiting distribution.

Changes in the balance of intra- and interspecific competition, resulting from severe habitat alterations, may have induced an ecological replacement of the eastern meadowlark by a better-adapted western species in certain areas.

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APPENDIX

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EGG CANNIBALISM AND FECUNDITY IN TRIBOLIUM

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Introduction

The study of population ecology is, in the final analysis, concerned with the interaction of three basic factors, namely; natality, mortality and dispersion. This is true of work in the field or in the laboratory; whether the approach is populational (concerned wth census trends), analytical (concerned with causal relations), or deductive (concerned with mathematical models). Natality, mortality and dispersion produce shifts of numbers in time which are observed in the reproducing population.

Flour beetles of the genus *Tribolium* are particularly favorable material for laboratory population study. Technical advantages and ecological characteristics make them suitable for detailed investigations of numerous problems at various levels of complexity. Some of the work which has been done deals with the relationship of a particular response and a particular factor or set of factors; for example, density and fecundity, or temperature and developmental rate. Such studies would generally be classed as "analytical." More "populational" are the studies in which the response of an entire population or mixed-species population is observed.

The work reported here is part of a program which is essentially an analytical study of the mechanisms operating within a population and resulting in what may be regarded as a dynamic population equilibrium. In particular the subjects of egg cannibalism and fecundity will be considered. This problem is important because egg cannibalism is, under conditions of high population density, an extremely powerful source of mortality. It is complex because the egg numbers are in a continual state of flux, simultaneously increased by ovipostion and decreased by cannibalism. Very little information can be obtained about the involved rates or the egg survivorship from data on the standing crop of eggs.

Chapman (1928) suggested that the imagoes eat their own eggs and Park (1934) actually described this behavior. Cannibalism of eggs has been shown to increase with increased adult density by Chapman (1928, 1933), Chapman and Baird (1934), Chapman and Whang (1934), Park (1933), Stanley (1942), Crombie (1944) and Boyce (1946). The increase in the number of eggs recovered per beetle per unit time, an index of fecundity, has been shown to decrease with increased adult density by MacLagan (1932), Park (1933), Crombie (1944) and Boyce (1946). The phenomenon of decreased reproductive rate under conditions of crowding has been observed in widely different groups of animals and various explanations have been offered in the specific cases.

A survey of the work on egg cannibalism shows clearly that the number of eggs destroyed is dependent upon the number of eggs present and the number of imagoes. This is, as pointed out by Allee *et al.* (1949), a simple, straightforward case of predation—the egg being the prey and the active form the predator.

Boyce (1946) concluded that while cannibalism is present, it plays a lesser role than the reduction of fecundity by crowding in the decline of the growth rate of a population. This view is opposed to that of Chapman and Whang (1934), who ascribe the major role to egg cannibalism. Birch, Park and Frank (1951) considered both fecundity and cannibalism under conditions of crowding of females by imagoes of their own species and by imagoes of another species. They concluded that there is a difference in the reduction of fecundity which results from crowding by males and by females. The crowding by females directly affects the fecundity, while the effect of crowding by males can be accounted for by cannibalism.

In a mixed-sex culture eggs are being added and destroyed constantly. It would of course be most convenient if cannibalism rates could be obtained from cultures containing only males cannibalizing introduced eggs, and then these data applied to the mixed-sex situation. In some of the work it was assumed that this procedure is valid; however, it was suggested by Stanley (1942) and Boyce (1946) that the rate of cannibalism may be higher for females than for males. In such a case, of course, the rate of cannibalism used would underestimate the rate in the mixed-sex cultures and lead to an underestimate of fecundity rates.

For the purposes of this discussion it will be convenient to agree on three definitions of terms which must be used repeatedly:

Net fecundity rate—the increase in the number of eggs which are observed or recovered per beetle in unit time.

Real fecundity rate—the number of eggs produced per beetle in unit time.

Cannibalism rate—the fraction of eggs present which are cannibalized per beetle in unit time.

This last definition is actually rather arbitrary. There are other minor causes of eggs being destroyed or effectively destroyed through puncture and collapse but it is not feasible to distinguish the actual case for each egg. Therefore all eggs which are missing, entirely or in part, are said to have been cannibalized.

All of the rates expressed here are based on a time interval of 24 hours. If the reader objects to the implication that males lay eggs, he may double all of the fecundity rates to put them on a per female basis.

The fecundity rates which are of populational interest are primarily those obtained under conditions of some crowding and with a sex ratio near unity. Boyce (1946) obtained an estimate of fecundity under these conditions. She plotted curves of the daily increment of eggs per adult against the egg density. By extrapolation the number of eggs appearing per adult per day at zero egg density was obtained. This value approximates the real fecundity (cannibalism being eliminated).

In the present work a technique is presented which consists of estimating the rate of cannibalism from the observation of the decimation of a known number of marked eggs. Simultaneously the number of eggs laid and recovered are observed. The real fecundity can then be calculated from the number of new eggs and the cannibalism rate. A deterministic model is adopted here for the calculation of both rates from a single set of data.

It is not the intent of this paper to attempt an evaluation of the roles of cannibalism and fecundity in the laboratory population, but only in a very much simplified situation. This is an analysis of the fecundity and cannibalism rates of beetles of known age and history, under essentially optimal and constant physical conditions.

This paper is, in essence, a thesis presented to the faculty of the Division of Biological Sciences of the University of Chicago in candidacy for the degree of Doctor of Philosophy. The work was done under the guidance of Professor Thomas Park to whom I wish to express my sincere gratitude. Others who helped in various ways and to whom I wish to acknowledge my appreciation are the following: John LeGay Brereton, Charles Kraft, Stephen Moszkowski, Alfred Naylor, Professor Jerzy Neyman, Robert Read, Mary Jane Rich, Elizabeth Scott, Valentine Telegdi and Professor Sewall Wright. Some of the modifications of the original thesis were made while the author was a postdoctoral fellow of the National Science Foundation at the Statistical Laboratory, University of California.

Experimental Design

In accordance with the experimental design the number of beetles and the duration of the observation period are manipulated. The number of marked eggs which are introduced is controlled at a constant level and the number of new eggs is always zero at the start of a period. The number of marked eggs and the number of new eggs which survive are counted. This information enables us to calculate the egg cannibalism rate and the real fecundity rate by means of a deterministic mathematical model. The equation for this model is not original, but has several applications in the field of physics.

Before deriving this equation let us make the following notation:

Let $b =$ number of beetles,
$c =$ rate of cannibalism per beetle,
$E =$ rate of oviposition per beetle,
$N =$ number of eggs present at time t,
$N_o =$ number of eggs present at time $t = 0$.

For a population of beetles, the rate of egg laying will be Eb per unit time; the rate of egg cannibalism will be Nbc per unit time. Therefore, as time changes, the number of eggs will change according to the relation:

$$dN = Ebdt - Nbcdt,$$

or, in terms of dt,

$$\frac{dN}{Eb - Nbc} = dt.$$

Equivalently,

$$-\,d\ln\,(Eb - Nbc)\frac{1}{Bc} = dt$$

which integrated is

$$\ln\,(Eb - Nbc) = -\,bct + K$$

or, with $k = e^K$

$$Eb - Nbc = ke^{-bct}.$$

When $t = 0$, $N = N_0$, hence

$$Eb - N_0bc = k.$$

Substituting this value for k,

$$Eb - Nbc = (Eb - N_0bc)e^{-bct}$$

and transposing, we obtain

$$N = N_0e^{-bct} + \frac{E}{c}(1 - e^{-bct}),$$

which is the general equation applied in the present work.

Certain assumptions are made in the application of the equation and it is useful to test these in order to establish the limitations of the method.

The first term N_0e^{-bct} of the general equation represents the number of introduced eggs which were not destroyed. The second term $\frac{E}{c}(1 - e^{-bct})$ is the number of new eggs which have been accumulated. It is to be noted that c, the fraction of eggs present which are destroyed per beetle per unit time, is a constant; it is independent of the other parameters and it appears in both terms of the equation. In hypothesizing that c is a constant, we make the assumption that the probability that a particular egg will be encountered and destroyed in any given time interval is the same for all eggs. It is implicit under this assumption that:

1. There is no non-random searching;
2. There is no phenomenon of "satiation";
3. Eggs of the introduced group and newly laid eggs are equivalent in their susceptibility to cannibalism;
4. Adult densty does not affect the rate of cannibalism.

In considering E a constant we are assuming that the fecundity rate is not affected by the adult density and does not change in time.

EXPERIMENT I. On the basis of existing evidence one would expect the rate of oviposition, and perhaps cannibalism, to vary with adult density. Those assumptions presented above concerned with the alleged lack of influence of adult density would therefore be unrealistic and an observed difference in the rates between different densities would confirm this. If the other assumptions (*i.e.,* those not referring to adult density) hold true, then (1) the values for cannibalism rates, calculated from the number of marked eggs recovered, should be constant relative to time interval within density and (2) the fecundity rates should be constant within a given density.

In order to test the assumptions a factorial experiment was designed using groups of beetles at 6 conditions of density over 6 time intervals. In this case the sex-ratio was unity. The design of this experiment is presented in Table I. There are 36 cells in the table, each one treatment; that is, a particular density of animals observed over a certain time interval. Each of these 36 treatments was replicated 10 times and each replicate was observed over three successive intervals of the specified length. In computing the rate values, the three successive time observations for each replicate were averaged. This was true for both the marked eggs which were introduced at the start and for the new, unmarked, eggs which were laid during the interval. The means for the former therefore are the number of marked eggs recaptured; for the later, the number of eggs laid which survived to be counted.

TABLE I. The design of the experiment testing for effects of time and density on rates of fecundity and cannibalism (numbers in cells show replication)

Time in hours	Density, Beetles per 8 grams of medium					
	8	16	32	64	128	256
8.......	10	10	10	10	10	10
16.......	10	10	10	10	10	10
24.......	10	10	10	10	10	10
32.......	10	10	10	10	10	10
40.......	10	10	10	10	10	10
48.......	10	10	10	10	10	10

In estimation of the cannibalism rate the equation, $M_t = M_0e^{-bct}$ was solved for c. M_0, the number of marked eggs introduced at the start of the period, was always 200. M_t is the number of those marked eggs which were subsequently recovered. The value of c was substituted, together with the average number of new eggs, N_t, in $N_t = \frac{E}{c}(1 - e^{-bct})$. This equation was then solved for E, the real fecundity rate. Thus we obtain from the original data estimates of c and E for each of the 10 replicates in the 36 experimental treatments. These values can then be examined in terms of the hypothesis to be tested: the rates of egg cannibalism and fecundity are constants.

EXPERIMENT II. Boyce (1946) and Birch, Park and Frank (1951) made the assumption that the rates of cannibalism are the same for males and females. This assumption is obviously important in the interpretation of their results on the effect of crowding on fecundity. Therefore, a second experiment was set up using the marked-egg recovery technique to test the hypothesis of equal cannibalism rates for males and females. Here, observations were made at one density, 32 beetles per 8 grams of medium, and one time interval, 24 hours. Five different sex ratios were used: 28 males: 4 females, 24 males: 8 females, 16 males: 16 females, 8 males: 24 females, 4 males: 28 females.

For the purpose of computing the cannibalism rates for males and females the equation for the estimation of cannibalism from marked egg data was modified to

$$^{-(b_fc_f} + M_t = M_0e^{\ b_mc_m)t}$$

Here the subscripts f and m indicate that the parameter applies to females or males respectively.

In this experiment the numbers of marked eggs recovered were fitted to a linear regression line of the form $M_t = \alpha + \beta x$ where x is the fraction of the population which are males. The values of M_t where $x = 0$ and $x = 1$ are thus estimates of the expectation of the number of eggs which survive when the population is composed exclusively of females or males respectively. To test the hypothesis of equal cannibalism rates for males and females it is sufficient to test the hypotheseis that $\beta = 0$.

MATERIALS AND METHODS

A method of marking eggs was devised so that it would be possible to distinguish the eggs which had been introduced at the beginning of the observation period from those which were laid during the period. At the time of oviposition the surface of the egg is covered with a moist, sticky substance. Flour particles adhere as this dries. When about one percent crystalline neutral red was added to the medium, the eggs were colored pink. The marked eggs are clearly distinguishable from normal white eggs.

It is conceivable that the application of the dye might in some way alter the "palatability" of the egg or cause it to be desiccated so that it would collapse. The following experiment was set up to check this point. Two groups of beetles, A and B, were used. Each group consisted of 16 males and 16 females. The beetles were placed in a vial of medium containing 200 eggs. The eggs were, on alternate days, marked or unmarked. Thus, for example, on day 1 group A was offered 200 marked eggs, group B was offered 200 unmarked eggs; on day 2, group A was offered 200 unmarked eggs and group B 200 marked eggs; and so on for 10 days. At the end of each 24 hour period the eggs were recovered and counted without regard to color. These observations are presented in Table II. The mean number of eggs which were recovered on those days on which marked eggs were offered was 258.6 ± 3.20. The mean number of eggs recovered when unmarked eggs were offered was 255.7 ± 3.20. The difference between these means (2.9 ± 5.1) is clearly not significant and there is no reason to suspect that marked eggs are either more, or less, subject to destruction than are unmarked eggs.

TABLE II. The total number of eggs recovered when 200 were introduced and exposed for 24 hours (density 32 beetles per 8 grams)

Eggs introduced	Group A		Group B		Sum of totals
	Day	Eggs recovered	Day	Eggs recovered	
200 marked	1	274	2	254	
	3	270	4	241	
	5	262	6	261	
	7	270	8	242	
	9	268	10	244	
	Total	1344	Total	1242	2586
200 unmarked	2	268	1	243	
	4	258	3	256	
	6	251	5	248	
	8	274	7	247	
	10	264	9	248	
	Total	1315	Total	1242	2557

The animals used in these experiments were obtained from a stock of *Tribolium confusum* Duval which has been maintained in the laboratory of Professor Park for approximately 25 years. All beetles were reared in mass cultures at relatively low density (4 to 6 per gram). The animals were sexed as pupae and within 2 days after eclosion were introduced into vials of medium at the densities and sex-ratios specified in the experimental design. The cultures, of various densities were then left in an incubator under the conditions of the experiment for 14 days. When the actual experiments were started the beetles were between 14 and 16 days of age and had spent almost their entire adult life under conditions approximating those of the experiment with regard to density, temperature and humidity.

All of the experiments were carried out at an average temperature of 29.02° ± 0.2°C and a humidity of 73.6 ± 0.8 percent. The medium used consisted of 95 percent whole wheat flour and 5 percent brewers' yeast. These ingredients were sifted through fine (no. 7) silk bolting cloth before being weighed and mixed. Eight grams of medium were weighed into shell vials and covered with coarse gauze. The prepared vials were then kept in the experimental conditions for 3 to 5 days before use. This period of acclimatization is necessary for the conditions of temperature and humidity within the flour to come to equilibrium with the experimental environment.

The typical procedure of experimental observations is as follows:

1. Two hundred marked eggs are mixed with 8 grams of fresh, acclimatized medium.
2. The population to be observed is removed from the incubator and the adults removed by passing the contents of the vial through a coarse (No. 00xx) bolting cloth sieve. Any dead beetles are replaced wth animals of similar age and sex.
3. The adults are placed on the top of the fresh medium to which marked eggs were added and the vial is replaced in the incubator.
4. Eggs are separated from the old medium by use of a fine (No. 2) sieve and spread on black

paper to be counted. A hand lens is used to help distinguish between normal eggs, both marked and unmarked, collapsed eggs, and flour particles.

It seems likely that in handling the eggs some might be lost or damaged. To assess this a series of counts were made on several groups of eggs. Two hundred marked eggs were counted and mixed with flour. After 24 hours the eggs were sifted and counted again. The counts at the end of each period were repeated three times in order to check the accuracy of counting. The range of error was found to be ± 2 eggs per 200, about one percent. The loss of eggs averaged about one half of one percent. These errors, so small in relation to the variability of the observations, are deemed negligible.

Experimental Results and Discussion

The records of the recovery of marked and unmarked eggs relative to density and time interval are summarized in Table III and Figure 1. The values presented are the means, together with their standard errors, and the coefficients of variability for the 10 replicates in each of the 36 treatments. Table III shows the numbers of marked eggs and new eggs recovered for each of the 6 densities and each of the 6 time intervals. Figure 1, a composite of individual graphs for each of the 6 densities, plots the number of eggs (ordinate) against time interval (abscissa). In all cases the broken line is the number of marked eggs; the solid line, the number of new eggs recovered.

The curves of Figure 1 indicate that the equation for the number of eggs is of the right general form. The number of marked eggs recovered shows a decrease with time interval which is more or less consistent over the various conditions of density. These curves have in common the characteristic that the amount of decrease in numbers, or the slope of the curve, is greater early in time than late. This quality is found in curves of the general type $y = e^{-x}$. This is the common "die-away" or exponential decay curve. Referring to the graphs of the number of new eggs recovered (solid lines) it is seen that the number of new eggs increases rapidly at first and then more slowly. When one plots the change of numbers against time, a curve of the same form as is observed in the case of marked egg recovery results. The curves of the number of unmarked eggs are compound in character. There is a tendency for linear increase, due to essentially constant fecundity, and a component of decrease which increases in its effect as the number of eggs increases. This is especially visible in the graphs of densities 128 and 256.

Table III. Recovery of marked and unmarked eggs relative to time and density (replication 10 in each case)

Density	Time	Marked eggs recovered		Unmarked eggs recovered	
		Mean S.E.	C.V.%	Mean S.E.	C.V.%
8 per 8 gm	8	192.7±1.0	2	14.2± 1.0	21
	16	191.3±1.3	2	33.8± 1.1	11
	24	188.0±1.5	2	46.4± 1.6	11
	32	186.7±2.1	4	57.9± 1.9	10
	40	186.2±2.5	4	81.7± 3.1	12
	48	182.6±3.2	6	93.4± 1.8	6
16 per 8 gm	8	188.8±1.5	3	28.5± 1.3	15
	16	183.2±2.6	4	61.4± 2.0	11
	24	175.4±2.5	5	86.8± 2.0	7
	32	174.8±3.1	5	114.2± 2.9	8
	40	165.5±4.7	9	148.6± 2.3	5
	48	171.6±3.1	6	173.8± 2.4	4
32 per 8 gm	8	181.6±2.4	4	47.4± 2.4	16
	16	164.8±3.5	7	100.8± 5.5	17
	24	154.6±3.9	8	155.8± 3.2	7
	32	148.2±6.2	13	191.7± 5.4	9
	40	136.7±5.7	13	242.5± 7.0	9
	48	138.5±6.1	14	274.3± 6.1	7
64 per 8 gm	8	169.9±3.4	6	79.2± 5.3	21
	16	150.7±3.9	8	156.0± 9.2	19
	24	126.9±4.7	12	226.5± 9.0	13
	32	126.6±6.6	16	282.7±12.1	14
	40	102.1±4.7	15	351.9± 9.9	9
	48	93.5±5.3	18	371.8± 7.6	7
128 per 8 gm	8	166.9±3.7	7	123.9±10.3	26
	16	135.2±5.2	12	205.4±13.0	20
	24	105.7±6.4	19	301.7±13.7	14
	32	94.6±4.6	15	367.9±22.1	19
	40	75.6±5.2	22	458.4±16.3	11
	48	66.7±5.5	26	467.6±16.8	11
256 per 8 gm	8	166.5±2.3	4	161.4±13.7	27
	16	118.6±5.6	15	282.6±16.3	18
	24	77.8±5.1	21	371.1±18.2	15
	32	73.6±5.1	22	447.9±23.2	16
	40	47.5±4.6	31	510.6±23.9	15
	48	41.3±5.2	40	552.4±22.4	13

The curves of Figure 1, while of the same two general forms, obviously vary with density. An examination of Table III emphasizes this change and further shows that the variability in the data, as indicated by the coefficients of variation, is not constant but varies in a systematic way from treatment to treatment.

The rates of cannibalism are presented in Table IV and Figure 2. The real fecundity rates are shown in Table IV and Figure 3. The rates expressed for a particular time interval are essentially average rates from time zero to the time of sifting. In Table IV the means of the cannibalism rates and fecundity rates are presented together with their standard errors and coefficients of variability for the 10 replicates in each of the treat-

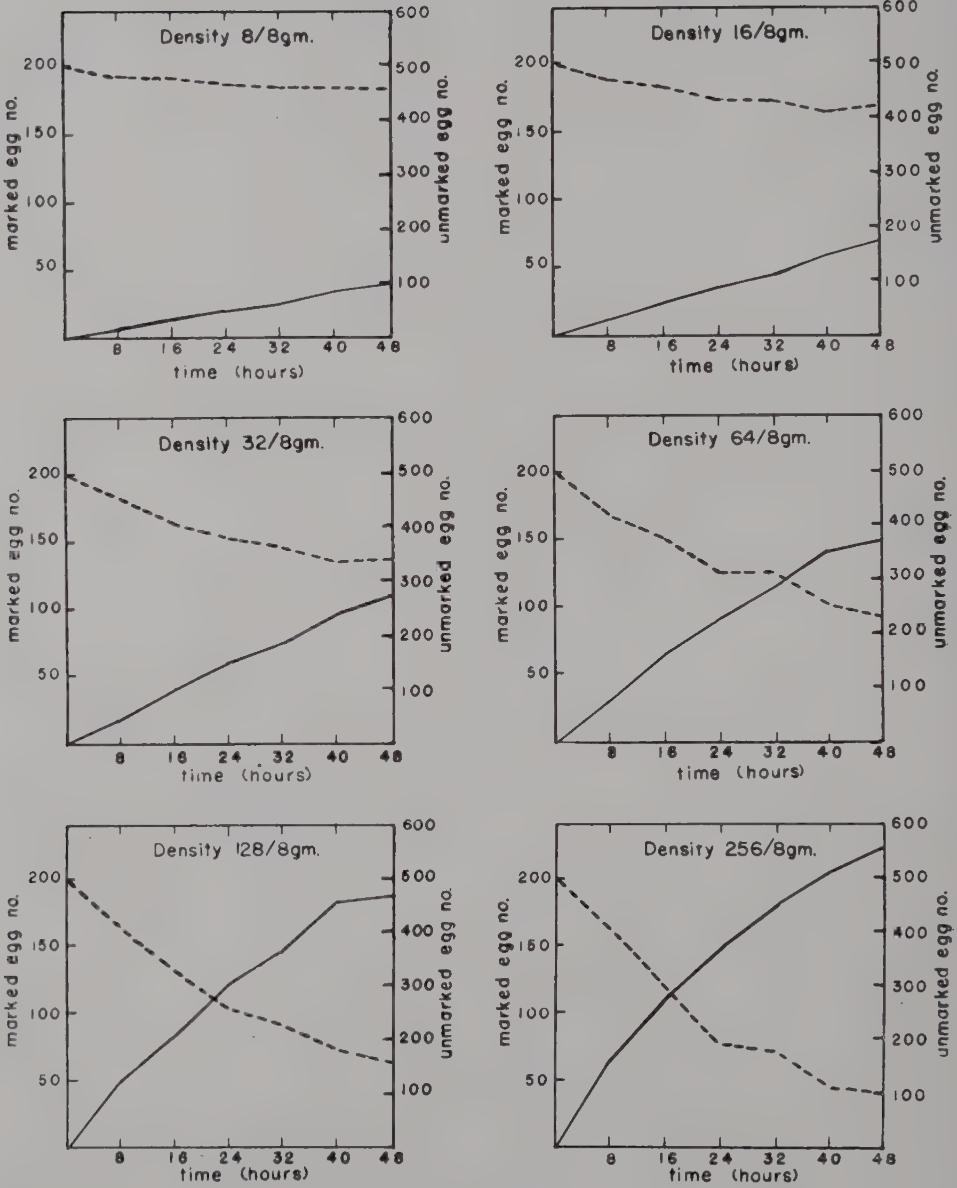
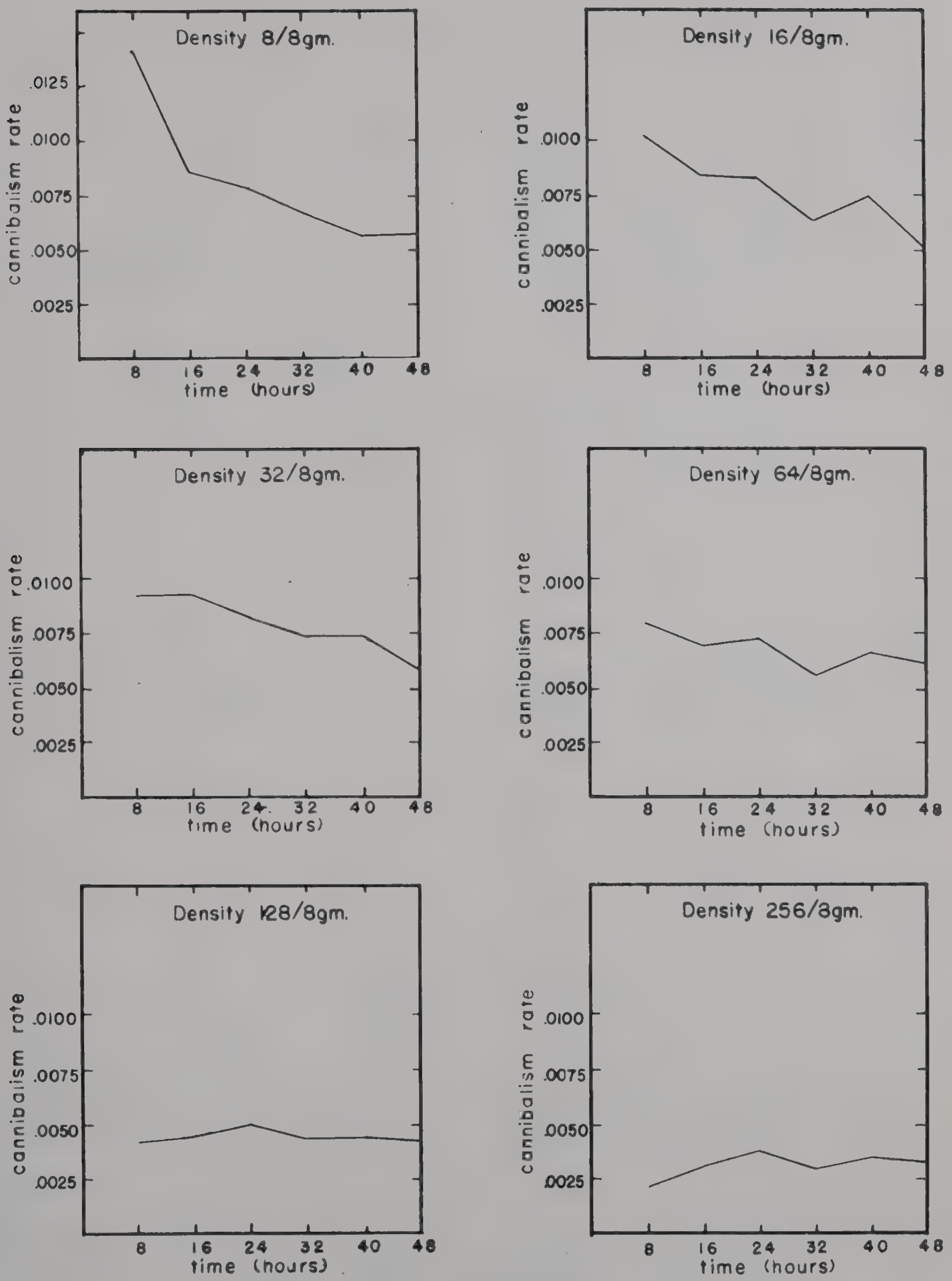


FIG. 1. Number of eggs recovered relative to time interval for each density (broken line—marked eggs; solid line—unmarked eggs).

ments. Figures 2 and 3 are again composites of 6 individual graphs each representing one density. In Figure 2 the cannibalism rate is plotted on the ordinate with time on the abscissa; Figure 3 similarly plots fecundity against time interval. Recall that under the fundamental assumptions of the model both rates should be constant. However, these means show clearly that the rates are not constant within density, between time intervals or within time interval, between densities. As density increases the table and graphs show these relations to hold: One, cannibalism as a rate per beetle decreases; two, real fecundity, again as a rate per beetle, decreases; and three, the reduction in each



Density 8/8gm.

Density 16/8gm.

Density 32/8gm.

Density 64/8gm.

Density 128/8gm.

Density 256/8gm.

Fig. 2. Cannibalism rate relative to time interval.

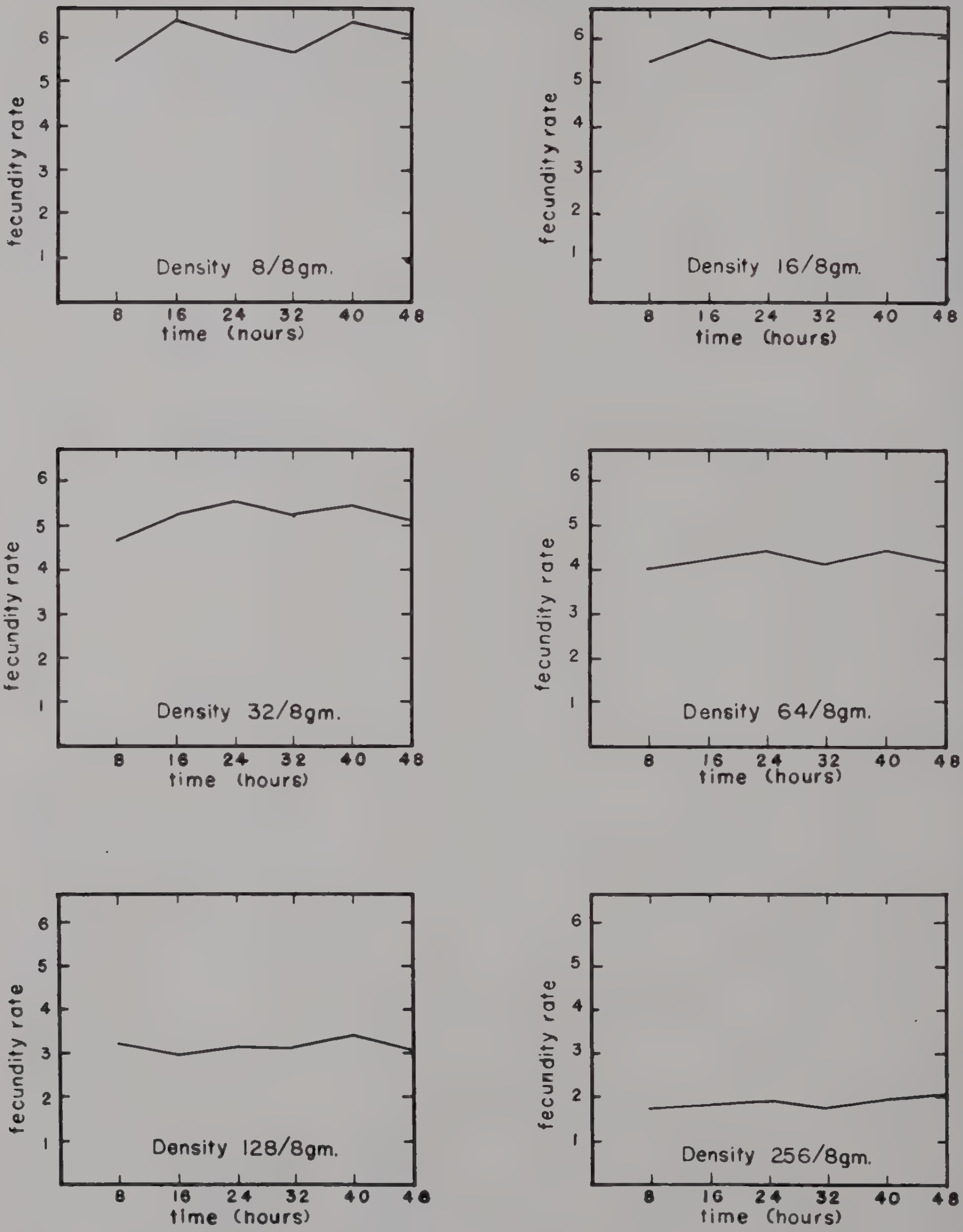


FIG. 3. Real fecundity rate relative to time interval.

of the two rates with increased density is similar. In illustration of these conclusions let us select from Table IV a specific instance. The rate of cannibalism at the density of 256 beetles to 8 grams of flour is about 37 percent of that observed at the density of 8 beetles per 8 grams. That is, the average rate of cannibalism at all times for all replicates at the highest density is 37 percent of the average rate at the lowest density. The fecundity rate at 256 beetles to 8 grams is 36 percent of the fecundity at the density of 8 beetles per 8 grams.

Table IV. Cannibalism and fecundity rates relative to time and density (replication 10 in each case)

Density	Time	Cannibalism rate		Fecundity rate	
		Mean S.E.	C.V.%	Mean S.E.	C.V.%
8 per 8 gm	8	.01399 ± .00192	43	5.42 ± .36	21
	16	.00838 ± .00131	49	6.45 ± .24	12
	24	.00775 ± .00098	40	5.98 ± .22	12
	32	.00654 ± .00104	50	5.65 ± .18	10
	40	.00542 ± .00100	59	6.35 ± .24	12
	48	.00579 ± .00114	62	6.11 ± .13	7
16 per 8 gm	8	.01083 ± .00151	44	5.50 ± .26	15
	16	.00830 ± .00139	53	5.96 ± .20	11
	24	.00822 ± .00091	35	5.56 ± .19	11
	32	.00638 ± .00083	41	5.71 ± .11	6
	40	.00730 ± .00101	44	6.16 ± .06	7
	48	.00484 ± .00057	37	5.86 ± .06	3
32 per 8 gm	8	.00913 ± .00127	44	4.65 ± .32	22
	16	.00918 ± .00091	34	5.21 ± .31	19
	24	.00813 ± .00079	31	5.52 ± .09	5
	32	.00722 ± .00104	45	5.21 ± .12	7
	40	.00729 ± .00082	36	5.42 ± .17	10
	48	.00588 ± .00069	37	5.15 ± .16	10
64 per 8 gm	8	.00774 ± .00094	39	4.03 ± .27	21
	16	.00671 ± .00061	29	4.22 ± .28	21
	24	.00719 ± .00055	24	4.42 ± .18	13
	32	.00550 ± .00059	34	4.14 ± .17	13
	40	.00639 ± .00045	22	4.54 ± .12	8
	48	.00605 ± .00041	21	4.18 ± .13	10
128 per 8 gm	8	.00430 ± .00052	38	3.20 ± .28	28
	16	.00468 ± .00049	33	2.93 ± .20	22
	24	.00511 ± .00046	28	3.23 ± .18	17
	32	.00445 ± .00030	21	3.08 ± .20	20
	40	.00465 ± .00031	21	3.39 ± .12	11
	48	.00440 ± .00031	22	3.06 ± .17	18
256 per 8 gm	8	.00216 ± .00016	23	2.07 ± .18	27
	16	.00313 ± .00029	29	2.14 ± .12	18
	24	.00377 ± .00027	22	2.25 ± .10	14
	32	.00299 ± .00020	21	2.10 ± .12	18
	40	.00347 ± .00023	21	2.29 ± .09	13
	48	.00321 ± .00023	23	2.33 ± .16	22

Table V. Analysis of variance—cannibalism rates

Source	d. f.	Sum of squares	Mean square	F	F .99	P
Total.........	359	4361	12.15	....	....	....
Treatments....	35	2030	58.00	....	....	....
Density.....	5	1197	239.41	12.40	3.86	<.01
Time.......	5	351	70.12	3.63	3.86	<.05
Interaction..	25	482	19.30	2.68	1.88	<.01
Discrepance...	324	2331	7.19	....	....	....

Table VI. Analysis of variance—fecundity rates

Source	d. f.	Sum of squares	Mean square	F	F .99	P
Total.........	359	832.95	2.32	....	....	....
Treatments....	35	711.58	20.33	....	....	....
Density.....	5	692.20	138.44	378.25	3.86	<.01
Time.......	5	10.24	2.05	5.60	3.86	<.01
Interaction..	25	9.14	0.37	0.98	1.88	>.05
Discrepance...	324	121.37	0.38	....	....	....

The decrease in the observed rates of cannibalism from the shortest to the longest time intervals for the various densities of imagoes are approximately as follows: 8, 50 percent; 16, 40 percent; 32, 30 percent; 64, 20 percent; 128 and 256, imperceptible. The errors introduced by the loss of eggs in collections would tend to be most important at the lower densities and over the shorter time intervals. These errors always cause an overestimate of cannibalism rates. In the most extreme case, that of a density of 8 beetles over a time intervals of 8 hours, the order of magnitude of the error is so small that only about 10 percent of the cannibalism rate, or 20 percent of the observed deviation could be accounted for.

Analyses of variance were carried out on the values for cannibalism rate and fecundity rate with respect to time and density (Tables V and VI). These show that cannibalism and fecundity rates are affected by time and density and that there is an interaction between time and density on the cannibalism rate. All of these relationships are significant at the arbitrarily chosen one-percent level except cannibalism rate and time ($P < .05$). We therefore reject the hypothesis that c and E are constants.

The change with density in the form of the cannibalism versus time curves (Fig. 2) is the obvious source of the significant interaction between time and density. The explanation of the significant effect of time on fecundity rate is not clear (Fig. 3). Since the cannibalism rates are used in the estimation of fecundity, one might expect some reflection of the cannibalism time trend in the fecundity rates. None, however, is apparent.

The use of analysis of variance here is perhaps questionable. The technique requires that the data be normally distributed and that the variance of the sub-groups be equal. Neither of these conditions are entirely met by the present data, so conservative tests were made in which the interaction term was used to test the significance of time and density rather than the more sensitive test using the discrepance.

The results of Experiment II on the recovery of marked eggs from cultures composed of various sex-ratios are shown in Table VII. The effective cannibalism rate here is simply the mean cannibalism rate ignoring the sex of the beetles, that is, it is equivalent to c as used in the previous section. If the rates of cannibalism were the same for males and females, the number of marked eggs recovered and the effective cannibalism rates would be the same for all five sex-ratios.

The data on marked egg recovery were fitted to a regression line $M_t = \alpha + \beta x$ where x is the

Table VII. Summary of the results of the experiment to determine cannibalism rates for males and females

	Mean no. marked eggs recovered	Effective cannibalism rate (mean)
28 males 4 females........	175.5±1.6	.00409
24 males 8 females........	163.0±2.1	.00615
16 males 16 females........	135.7±3.9	.01211
8 males 24 females........	124.9±3.8	.01472
4 males 28 females........	117.5±4.3	.01632

fraction of males in the culture. The resulting estimates for α and $\alpha + \beta$ are respectively the expected numbers of eggs when the population is all females or all males. The test of equal cannibalism rates for males and females is the test of the hypothesis $\beta = 0$. This hypothesis is rejected at the one-percent level by t-test. The estimated cannibalism rate for males is .002983 ± .000068 while the rate for females is .020119 ± .000073. The ratio of female rate to male rate is approximately 6.8.

Since the rates of egg cannibalism vary with the length of the period of observation it seems clear that the situation assumed in the model only partly reflects events in the population. This model is, as is usually the case, an oversimplification. It is interesting, and perhaps profitable, to speculate on the possible reasons for the differences between the model and the empirical findings.

While it has been shown that marked and unmarked eggs are equally subject to cannibalism, there is one point of notable difference between the marked and unmarked eggs in these experimental conditions. The marked eggs are distributed in the flour by hand more or less at random and the distribution of these eggs can be assumed to be Poisson. The beetles are placed on top of the flour in the vial, burrow into the medium and proceed to establish a more or less stable pattern of interconnected tunnels. The rate of tunnel formation probably decreases as the number of tunnels increases. Since the beetles tend to re-use the tunnels it seems reasonable to suppose that the medium in the immediate vicinity of the tunnels will become nearly depleted of marked eggs. Therefore the rate at which the marked egg population is being decimated will decrease because the movement of the beetles is to some extent limited to those regions in which it is least likely for a beetle to encounter marked eggs. At the same time that the number of marked eggs in the vicinity of the tunnels is decreasing, relatively great numbers of new, unmarked eggs will be oviposited in this area. Under these circumstances the rate of cannibalism derived from marked-egg data will be an underestimate of the rate of cannibalism of new eggs; real fecundity rates therefore will be underestimated.

The problem of retunneling is discussed by Stanley (1942). He postulates a differential effect on egg numbers resulting from retunneling by males and by females. In the case of sex ratios unequal to one, the egg numbers would tend to increase if females were in excess and to decrease if males were in excess. However, since the sex-ratio in *Tribolium* populations is usually near unity, Stanley concludes that this retunneling effect is not important. With this general conclusion I of course agree. However, in the case presented in this paper the significance of retunneling cannot be disregarded because the possibility exists that marked and unmarked eggs may have different distributions.

Such a mechanism as the above would account for the type of deviations which have been observed in the present material. When the experiments were started it was anticipated that an independent estimate of the cannibalism rate could be obtained from the new egg data. This is theoretically possible where information is available over different time intervals for the same density. Unfortunately the data are too variable to permit the calculation of reliable estimates.

Although the rate of cannibalism decreases with increased adult density, it does not, at least over the range of densities considered here, decrease so much that it ceases to be a very powerful source of egg mortality. If it is assumed that the duration of the egg stage is 5 days and that all eggs are fertile, the number of eggs at equilibrium can be estimated as can the number of larvae expected per day. The increase to equilibrium is shown in Figure 4. The broken portion of the lines indicates the increase which would be expected in the absence of hatching. The number of larvae expected is equal to the number of eggs expected at day 6 minus the number of eggs at day 5. The number of larvae which would be expected at each density are as follows: 8, 33.8; 16, 47.3; 32, 42.4; 64, 26.8; 128, 16.1 and 256, 7.1.

Conclusions

It is concluded that both the rate of cannibalism (the fraction of the eggs present that are destroyed per beetle in unit time) and the real fecundity rate (the number of eggs laid per beetle

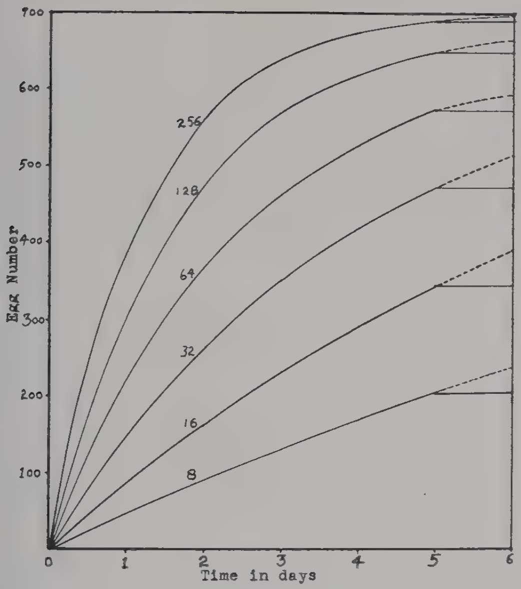


FIG. 4. Projected egg accumulation in time for various densities of adults.

in unit time) are similarly reduced by the increased density of beetles. It is further concluded that the decrease in net or apparent fecundity (the number of eggs per beetle recovered in unit time), which has been observed by various investigators, is largely due to the increase in the number of eggs cannibalized at higher densities.

From the observations made on cannibalism at various sex ratios it is concluded that females eat eggs at a much greater rate than do males.

The technique of marked-egg recovery offers a convenient method for the investigation of various problems connected with cannibalism and fecundity studies. At fairly high densities the method is quite reliable. The equations can be easily modified to assay fecundity and cannibalism in a reproducing population. For example, when all developmental stages are present in a population the following equation can be applied:

$$N_t = N_0 e^{-mt} + \frac{Eb}{m}(1 - e^{mt})$$

where m is an index of cannibalism rate for the entire population. The value of m would be derived from marked egg recovery data.

A definite problem in the work discussed here is the great variability. This may be due to the methods used, genetical factors and environmental conditions. By way of illustration of the latter it is interesting to compare the total number of eggs recovered in two similar situations. Consider 32 beetles in 8 grams of flour over a period of 24 hours. The figures appearing in Table II are from two groups of beetles which were reared together under conditions of rather high density. The average number of eggs recovered here is 257 and the range is quite small. The information in Table III for comparable density and time of observations comes from ten populations which were raised at different times under supposedly uniform conditions of low density. Here the average number of eggs recovered is 310 and the variability is considerable. The strong influence of environmental conditions, not only at the time of observation but also during the previous history of the animals, which is indicated here, makes it clear that the values which have been obtained in this study cannot be interpreted as "biotic constants" in the sense that R. N. Chapman and various other ecologists have used the term.

SUMMARY

A technique of assay of egg cannibalism and real fecundity rates is presented. Measurements of the decimation of a known number of marked eggs and the accumulation of new, unmarked eggs are made. These values are substituted into equations which are then solved for the rates. The equations are from a deterministic mathematical model which is borrowed from the field of physics. This model involves certain assumptions which are of biological importance and in the course of experiments conducted to test these it was found that:

1. The rates of egg cannibalism and real fecundity are similarly reduced by adult crowding;
2. The rates observed are not constant in time and it is postulated that this may be due to the relation between egg distribution and the pattern of beetle movement;
3. Cannibalism is an extremely important source of mortality and is of sufficient magnitude to be a major force regulating population growth;
4. Females eat eggs at a much greater rate than do males.

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THE ACORN MICROSERE, WITH SPECIAL REFERENCE TO ARTHROPODS[1]

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INTRODUCTION

The decay of an acorn follows a more or less predictable series of changes from the time the nut drops to the ground until it is incorporated into the humus of the forest soil. This succession is similar in many ways to that found in other decaying materials and in the major communities. Like the latter, it can be set off into stages that are indicated by breakdown of the various tissues and, roughly, by the animal and plant inhabitants of the nut. Study of succession in these small portions of the forest floor is aided by the rather definite boundaries and structure, the integrity of which is not destroyed by handling. Moving acorns to the laboratory offers little disturbance to the contents, and they can be maintained in the laboratory under controlled conditions for close study of the processes of decay and of the many organisms associated with them.

These nuts offer an unusual opportunity for study of the biotic interrelationships of a small part of the major community (O. Park in Allee *et al.,* 1949). The present work is an attempt to define these complexities of interaction and habit for all the organisms associated with acorn decay. Only by the accumulation of such studies can the make-up of any major community be eventually shown (Needham 1948).

I wish to express my sincere thanks and appreciation to Dr. Orlando Park for his guidance and criticism throughout this work and to the many taxonomic specialists without whose assistance this work would have been impossible. The identification of Acarina by Dr. Joseph Camin and Dr. H. H. F. Nesbitt was especially valuable.

REVIEW OF THE LITERATURE

In the period since the concept of the major biotic community was first proposed by Möbius in 1880 (Allee *et al.* 1949), no one has been able to demonstrate the complete interrelationships within any natural community. Because of the great complexity of these interrelationships, Elton (1947) suggested the study of the relatively simple community types, such as desert or tundra. However, many animal ecologists, from Shelford (1913) on, have attempted to study parts or phases of the forest; this work may some day be synthesized into a relatively complete picture.

The study of microhabitats and the successional changes there has provided useful information toward this synthesis of the larger problem, though there has been too little such study. It is typified by work like that of Savely (1939) on log decay, of Jacot (1939) on the role of mites and fungi in the breakdown of pine needles and dead roots, and of Mohr (1943) and Fuller (1934) on the succession of insects in dung and carrion. The parallel between log decay and tree-hole formation was pointed out by Park *et al.* (1950) with further elucidation of animal interrelationships in tree-holes by Park and Auerbach (1954).

The fact that acorns make up a large percentage of the fall and winter diet of many birds and mammals is pointed out by Van Dersal (1940 and others, and foresters (Korstian 1927) have investigated the factors which prevent the successful sprouting of the nut. Murtfeldt (1894) listed and described the life cycles of some of the larger insects which invade acorns. Some of her information is incorporated into the description of the activities of the initial animals which are discussed below.

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[1] Presented in partial fulfillment of the degree of Doctor of Philosophy at Northwestern University.

Materials and Methods

All acorns used in this study were those of *Quercus rubra* collected in Carlé Woods, Des Plaines, Cook County, Illinois. This is a red oak-sugar maple flood-plain forest (Braun 1950) on the bank of the Des Plaines River. Private ownership has kept disturbance to a minimum and the dense tree cover and close proximity to the river have resulted in a maximum of leaf litter and quite constant ground moisture, though actual flooding did not occur during the year of collection or for at least the two previous years.

Weekly collections were made from August 1950 to September 1951. Acorns were taken immediately to the laboratory and divided into groups at random, except that nuts in all stages of decay were included in each group. Some were placed in collecting apparatuses, some saved for dissection, and the remainder preserved in 95% alcohol. Those obtained in late fall and winter could be stored at four degrees centigrade, but at other seasons this was not possible because the animals were not adapted to low temperatures.

Several methods of collecting the animals were tried, but none proved as accurate, or tedious, as hand-picking under the dissecting microscope. A six-inch Berlese funnel, in which 50-100 nuts were broken up, served only as a qualitative check. This points up to the possible inaccuracy of this method for the quantitative extraction of arthropods from woody materials. At Dr. Park's suggestion, a "Microberlese" system was tested. This consisted of small funnels which narrowed down to a five-eighths inch opening, with a screen just above the constriction. Single nuts were broken open, placed on damp excelsior, and covered with the same material to slow the drying process. The intensity of light, covering, and other factors were varied, but no combination proved satisfactory, even qualitatively. Examination always showed that most of the smaller forms were trapped inside the shell, as was also found to be the case in the larger funnel. It is hoped that a method such as this might be perfected, for dissection of the acorns is an extremely slow process.

All the insect larvae had to be reared to the adult stage for identification. This was accomplished by placing nuts containing larvae on damp sand or cotton in jars or vials; soil was substituted for sand to allow the *Curculio* larvae to pupate. High humidities were maintained by keeping the containers in moist chambers. Shell vials were useful for keeping nuts under observation in optimum conditions. A saturated plug of cotton in the bottom kept the moisture high without having the nuts immersed in water. This provided contact with a moist substrate which seemed to give optimum conditions for the hygroscopic shells. An important feature of this method is that surface examination could be made without exposing the animals to dry conditions.

Many of the fungi, mites, and Collembola were cultured on agar slants in which acorn shells had been ground into non-nutrient agar. In some cases, nutrient agar was as successful, because many of the mites and Collembola feed on molds and bacteria. This method has good possibilities for culturing mites for observation, nutrition, and life-history studies.

Dissection of the acorns requires one to be somewhat of a detective. Not only is it important to be able to identify the organisms present at the time, but one must also know which ones had been there before. By the identification of feces, head capsules, pupal cases, type of entry and exit holes, and other factors one may, with experience, work out the sequence of events leading up to the time of examination. In most nuts up to late stage IV (see below), there are enough records left of the previous occupants to allow an almost complete reconstruction of the past history of any given acorn.

Description of the Acorn

The diversity of tissues makes a detailed description of the acorn of *Quercus rubra* necessary for an understanding of the stages and processes of decay (Fig. 1). Acorns of the red oak are readily distinguishable from those of all other oaks by the generally large size and the flat, shallow cup which always covers less than one-third of the shell.

The pericarp, or shell, is made up of five distinct layers (Korstian 1927). Outside are two single-celled layers, the first of heavily cutinized, cuboidal epithelium, the second of thin-walled parenchyma cells. Next is a deep (0.35-0.5 mm) layer of thick-walled sclerenchyma cells, somewhat elongate distally, grading into cuboidal to the inside. This yellowish layer is the hard, resistant portion of the shell and cytochemical tests showed it to be made up largely of lignin. The bulk of the pericarp is made up of layers of large thick-walled parenchyma cells and scattered groups of stone cells. The walls of the former are largely cellulose, with little lignification apparent. This parenchyma layer, averaging 3.5 mm in thickness, is very important as a source of food and as a hiding place for many animals. On the inner surface is a single layer of epidermal cells from which arise, as cellular extensions, the fibers forming the thick, inner mat characteristic of the black oak group.

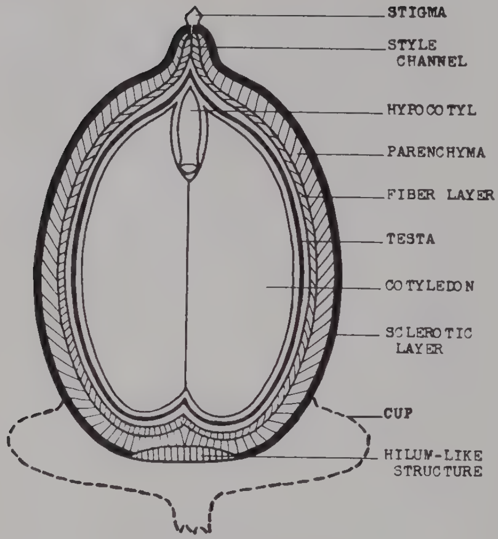

FIG. 1. Diagrammatic longitudinal section of a typical acorn of *Quercus rubra* L. x3.

The embryo, made up largely of the fleshy cotyledons, fills the cavity of the nut. It is surrounded by the testa, a thin, dark-brown membrane made up of several layers of small parenchyma cells. The large cells of the cotyledons are filled with oil droplets; it is this tissue which provides the major source of food for the organisms which initially invade the nut. The preceding histological description is based on that given by Korstian (1927), and sections of these tissues were subjected to confirmatory tests for the presence and distribution of cellulose, starch, lipids, and lignin. Procedures were those outlined by Meyer and Anderson (1941).

The cup is made of successive layers of suberized bracts surrounding a woody central axis containing the vascular tissues which supply the nut. It it attached to the hard, star-shaped "hilum-like" structure (Fuller and Tippo 1949) in the base of the nut.

In May of the second season after pollination, the embryo begins to form. From July onward there is a light but steady fall of immature nuts containing dead or aborted embryos. By the end of August and through September, mature nuts start falling in large numbers to remain dormant on the ground until the following Spring (Langdon 1939).

The interior of acorns provides a favorable habitat niche for the organisms associated with decay. The embryo and parenchyma provide a plentiful supply of food and the hard outer layer affords protection from predators and from sudden changes in the environment. The high moisture content of the floor stratum of Carlé Woods insures high humidities within the nuts, for the shells are quite permeable to water (Korstian 1930). This is well correlated with the fact that most of the organisms require humidities close to saturation. The organisms in the central cavity and parenchyma are somewhat independent of outside conditions until a large break occurs in the shell. Acorns provide a habitat niche which is dark, relatively moist, relatively cool, well supplied with food, and somewhat protected from the outside environment.

STAGES IN DECAY

In order to make study of the succession in decaying acorns more accurate, stages were defined to cover periods marked by the more obvious changes in different parts of the nut. These stages (Fig. 2) follow the system used by Savely (1939) on log decay. Though the arbitrary limits of the stages give an impression of activity only in the tissues concerned, it should be borne in mind that decay is in progress in all tissues at the same time; the different rates of breakdown allow for a definite sequence. Under certain conditions, this sequence of events may alter or the stages may be telescoped with two or more occuring at the same time. Even though there is a great variation in the specific patterns of decay, the general succession is followed in most of the nuts.

The stages set up are as follows:

Stage I includes the living nut, on or off the tree, in which any damage present would not, at a given point, prevent development of the embryo.

Stage II covers the period of destruction of the embryo. The shell layers are usually under attack during this stage, but this is seldom evident macroscopically.

Stage III includes the decay and breakdown of the inner shell layers, parenchyma and fibers, and the reduction of the mass of feces and dead embryo tissue left from stage II.

Stage IV covers the later decay of the woody outer shell and the cup; it is reached when these parts are softened enough to be broken easily in the hand.

Stage V is the mounding stage when the shell has lost its shape and identity and is being incorporated into the humus of the soil.

CHECK LIST OF ORGANISMS

The following is a list of all the organisms observed in the acorns collected in Carlé Woods. Many of these are of little significance, but it was

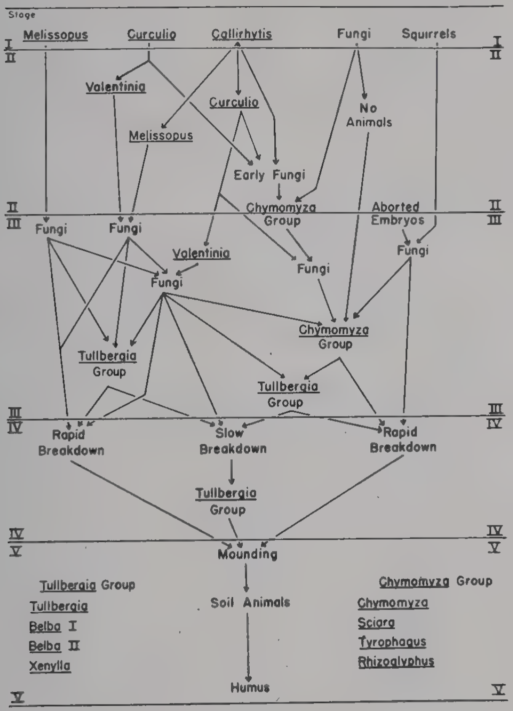

Fig. 2. Pathways of decay in acorns of *Quercus ruba* L.

felt that inclusion of all might be useful. The list of microorganisms is, of necessity, quite incomplete. The letters after the names of animals indicate food habits as far as is known, as follows: H—herbivorous, M—mycetophagous, Par—parasitic, P—predaceous, Sc—scavenger. These follow roughly the terminology of Brues (1946).

SCHIZOPHYTA: Bacteria, several unidentified species; Actinomycetes, *Streptomyces* sp.; (Fungi), Phycomycetes, *Pythium* sp., *Mucor* sp., *Rhizopus* sp.; Entomophthorales, two species; Ascomycetes, *Trichothecium roseum* (Tode) Harz, *Verticillium* sp., *Gliocladium penicilloides* Corda, *Phomopsis* sp., *Botrytis* sp., unidentified species; Basidiomycetes, *Armillaria mellea* (Vahl.) (Quel.), *Chaetomium elatum, Memnoniella echinata,* unidentified species; Deuteromycetes (Fungi Imperfecti), *Pestalozzia* sp., *Vermicularia* sp., *Alternaria* sp., *Penicillium* sp. I, sp. II, *Aspergillis* sp., *Fusarium* sp. I, sp. II, *Trichoderma lignorum* (Tode) Harz.

ALGAE: Chrysophyta, *Synura* sp.; Pyrrophyta, *Chilomonas paramecium* Ehr.

PROTOZOA: Ciliata, *Colpoda* sp., *Oxytricha* sp. (P).

NEMATODA: many species.

ANNELIDA: Enchytraeidae, Lumbricidae (Sc).

MOLLUSCA: Pulmonata, *Derocerus* sp. (Sc).

CRUSTACEA: Isopoda, *Trachellipus rathkei* (Brandt) (Sc).

CHILOPODA: Geophilidae, *Linotenia fulva* (Sager) (P), *L. chionophila* (Wood) (P).

ARACHNIDA: Tardigrada; Chelonethida, *Microbisium confusum* Hoff (P); Araneae; Acarina, *Tydeus* sp. (P), *Bdella* sp. (P), *Eupodes* sp. (M), *Tarsonemus simplex* Ewing (M), *Phthiracarus* sp. (Sc and M), *Belba* sp. I (Sc and M), sp. II (Sc and M), *Scheloribates* sp. (Sc. and M), Eulohmannidae, one species (M), *Tyrophagus lintneri* (Sc and M), *Rhizoglyphus rhizophagus* (Banks) (Sc and M), Phytoseiidae, one species (P), *Parasitus* sp. I (P), sp. II, Gamasellus sp. (P).

INSECTA: Collembola (Poduridae), *Xenylla grisea* Axelson (M), *Tullbergia iowensis* Mills (M and Sc), (Entomobryidae), *Folsomia fimetaria* (L.) (M), Sminthuridae; Corrodentia (Atropidae), *Liposcelis divinatorius* (Mueller) (Sc); Coleoptera (Genuina) (Carabidae), larva (unidentified) (P), (Staphylinidae), *Gyrophaena* sp. (P), (Cucujoidae), larva (unidentified), (Nitidulidae), *Stelidota octomaculata* Say (M and Sc), *Stelidota* sp., (Lathridiidae), *Cordicaria* sp. (Sc), (Pyrochroidae), *Neopyrochroa flabellata* (Fab.) (Sc); Rhynchophora (Curculionidae,) *Curculio rectus* Say (H), *Conotrachelus posticatus* Boh. (M and Sc); Lepidoptera (Blastobasidae), *Valentinia glanduella* (Riley) (Sc and H), (Olethreutidae), *Melissopus latiferreanus* (Wals.) (H), (Phycitidae), *Moodna ostrinella* (Clemens) (Pupates, only, in nuts); Diptera (Psychodidae), *Psychoda* sp. (Sc and M), (Itonidiidae (= Cecidomiidae)), *Rubsaamenia* sp. (M), *Mycodiplosis* sp. (M), *Miastor* sp. (M), (Sciaridae (= Mycetophilidae)), *Sciara coprophila* Lintner (M and Sc), (Drosophilidae), *Chymomyza amoena* (Loew) (M and Sc), (Anthomyiidae), one unidentified species; Hymenoptera (Formicidae), *Myrmecina americana* Emery, *M. punctiventris* Roger, (Cynipidae) *Callirhytis* (*fruticola?*) (H), (Encyrtidae), *Copidosoma* sp. Par (on moth larvae, polyembryonic)), (Braconidae), *Chelonus* sp. (Par (on moth larvae)).

Stage I

This stage covers the period during which the embryo is alive and undamaged or damaged only slightly. It is possible that some of the latter might develop (Korstian 1927), but no sprouted acorns were found in which any initial organisms had entered the nuts. It was found that insects entering the nuts carried pathogenic fungi to the interior, thereby introducing agents which invariably killed the embryo even though the insect itself did not. Because of this, breakdown and decay are initiated during this stage.

Several of the initial organisms attack the acorns while they are still on the tree. Numerically, the most important of these is the weevil *Curculio rectus* Say. The adult female bores through the pericarp and into the embryo with her elongate mouth parts and then deposits an egg in the hole. Upon hatching the young larva begins to tunnel through the embryo, consuming about half of it in the course of development, thus carrying the nut into stage II.

The adult moth *Melissopus latiferreanus* lays her eggs on the outside of the nut and the small, active larva chews a hole through the shell (Murtfeldt 1894). The feces left by this larva are in the form of hard, dry pellets which, unlike that of the weevil larva, are a poor source of food for animals. These moth larvae usually require the embryos of two or three nuts to complete development. Nuts entered by this form are thus in stage III when they drop to the ground and the exit hole is large.

A small percentage of the acorns contain larvae of *Callirhytis* sp., a cynipid wasp, two to eight soft white larvae to a nut, each in an individual gall in the embryo. These galls have extremely hard, resistant walls which protect the larvae to an amazing degree. As an example, 100 nuts were kept dry in a jar for 18 months; at the end of this period, no other animals were found alive, yet wasp larvae appeared normal when removed from the galls. None survived removal to even a saturated environment for more than two days, however; the resistance must be in the lignified layers of the galls. Decay of the rest of the nut goes on around the galls with no apparent effect on them.

Of the fungi which were identified in the acorns, only a species of *Penicillium* and one of *Fusarium* were found to initiate decay. These enter the nuts through the style channel, around the edges of the "hilum," and on the larvae of two species of itonidid flies, *Mycodiplosis* sp. and *Rubsaamenia* sp. Frequently, there was an obvious spread of growth outward from the areas occupied by these mycetophagous larvae; all the latter examined had large numbers of spores on the body surfaces. The space between cup and shell was usually occupied by some of these larvae and fungi, even in viable nuts; it is thought that the molds soften parenchyma tissues around the "hilum" enough to allow the larvae to enter. Another possibility is that the fungi, and possibly the immature dipterans, enter through the vessels of the "hilum" which lead into the embryo; some infections indicated this strongly. The fungi gradually turn the embyro brown and leathery from which condition there are two possible pathways of decay, with or without animals (see Fig. 2).

Of the initial fungi, *Penicillium,* at least, seemed to have a decided effect on both weevil and moth larvae. In all nuts containing these forms in which the fungus had throughly invaded the embryo, the larvae were stunted and failed to develop further. It is possible to speculate that *Penicillium* exerts an inhibitory effect on bacteria of the gut or gut cells. Bacteria were found in the gut contents and may be important in the nutrition of the larvae, as was found for some insects by Mansour and Mansour-Bek (1934). The only other instances of stunting occurred when three weevils or one *Melissopus* and one weevil were present. Then one of the weevil larvae was always much smaller than normal, presumably from lack of food.

Gray squirrels are an important factor in the breakdown of acorns in Carlé Woods, though the relative percentage of nuts taken by them was not determined. In breaking up the shells, these mammals destroy the central cavity and leave the fragments in essentially the same conditions as twigs and other small scraps of wood. This aspect of decay was not considered in this study.

On several occassions in the Fall, squirrels were observed collecting nuts in the following manner. An acorn would be picked up and smelled. If it was not discarded then, a small bite was usually made in the shell and the nut either cast aside or taken up into a tree, presumably for storage. All the discarded acorns examined contained larvae or fungi in the embryo, which would make them poor material for storage for any length of time. It is possible that the larvae and fungi cause a change in the odor of the embryo, as was found in chestnuts by Brooks and Cotton (1929).

The importance of the two species of Itonididae was impossible to evaluate other than as agents for the spread of spores. However, it seems that the great numbers which were frequently present, up to 50, in and around the embryo, would have some effect on the acorn as a whole.

Thus decay is initiated in stage I by several different organisms, all of which bring the nut into stage II by killing the embryo. There are probably other mammals, besides squirrels, and some birds which feed on these acorns; but none were observed to do this by the author.

STAGE II

During this period, the embryo is destroyed completely or partially by the initial organisms and other animals and fungi enter the nut, continuing the breakdown. Decay of the outer shell layers and parenchyma are usually initiated during this time, though there is little visible change. The shell layers are still too hard to be opened by hand and only in a few nuts have animals penetrated into the parenchyma layers.

Weevil larvae cut a characteristic exit hole in the shell, making the central cavity accessible to the mycetophages and scavengers which always follow. The most important of these is a moth, *Valentinia glanduella,* which lays eggs on or in the exit hole. When the larva hatches, it enters, and proceeds to spin a fine, tough web over the opening. This serves effectively to exclude many other animals which would otherwise invade the central cavity. This larva feeds on the remainder of the embryo and on the feces of the previous occupant, reducing them to dry, fibrous pellets similar to those left by *Melissopus,* the other moth larva. Development takes about one year, though there are indications that this is controlled by the amount of food available. Most eggs are laid in the Fall when weevil larvae are emerging. A behavioral study of the adult females is planned, especially as to egg laying.

Several species of fungi, especially the noncellulose decomposers, become established in the central cavity during late stage II. Most of these serve as food for the cheese mites, *Tyrophagus lintneri* and *Rhyzoglyphus rhyzophagus* and for dipterous larvae such as *Sciara coprophila* and *Chymomyza amoena,* which are frequently present at this time, though still in small numbers. The itonidid larvae invade the parenchyma, spreading fungus spores to this area. Cheese mites are also to be found on the outside of the shell under very damp conditions.

Stage II is the shortest of the periods of decay, sometimes lasting only a few minutes when a squirrel eats the nut, to the several weeks of the development of *Curculio* larvae or the action of fungi on the embryo. Because of the small number of viable nuts found, it is thought that most acorns in Carlé Woods pass through stage II while still on the tree, though the numbers taken by squirrels on the ground may be high.

STAGE III

During stage III, the parenchyma tissues are broken down, any remaining embryo tissues are reduced to feces, the central mass of feces and fibers is reduced, and decay of the hard sclerotic layer becomes evident. The parenchyma is invaded by fungi in late II or early III, and then this thick layer of large cells gradually separates into two parts. This is due partly to the action of molds and partly to that of various animals. Molds are introduced by the two itonidid larvae which are usually the the first animals into the region. They are to be found in the cells, oriented with the long axis. These small, flattened larvae probably chew out the end walls between the cells to go from one to the next. Solid matter other than molds is present in the gut contents of these larvae only here in the parenchyma and that in small amount. In view of feeding habits in other parts of the nut, it is probable that little of this is digested. Progression of these larvae through the parenchyma precedes the above-mentioned separation but it seems to be one of the causes for it.

As the parenchyma begins to separate and cell walls are further softened, the collembolans, *Tullbergia* and, to a lesser extent, *Xenylla,* move in. The depressed shape of these small insects makes for easy access to the spaces available. The former species feeds on both fungi and cellular materials, thus contributing to breakdown of the parenchyma. Examination of the feces showed large amounts of the substrate materials as well as mold spores. *Xenylla,* on the other hand, in feeding exclusively on spores and mycelia, contributes little or nothing to breakdown. This was well shown with agar slant cultures in which *Xenylla* starved after the surface molds had been cleared off, while *Tullbergia* tunnelled into the agar to a depth of one to two millimeters, ingesting the agar and contained nutrients as well as mycelia and spores.

If the acorns are very wet, both species of cheese mites move into the parenchyma as the central mass becomes depleted. The presence of these forms is always correlated with near-saturation of the tissues and considerable softening by fungi. In all acorns examined, these mites were invariably found in the wetter and softer areas, while the collembolans and oribatid mites were on the dryer (though still moist) and firmer substrates. In many instances individuals of both these groups were found in the same acorns because part of the parenchyma was rotted considerably while the rest was in an earlier stage of decay. Competition between them is a definite thing, but it takes a considerable time for any one species to become dominant. However, it is possible that the substrate is changed before one or another species becomes dominant over another. Further study on this is planned using various combinations of these microarthopods, for the agar slants show promise of being useful for this purpose. For the most part, the presence or absence of any species in a nut seems to be due primarily to the chance of invasion.

Of the insect larvae, none of the initial forms normally feed in the parenchyma, but those that follow, *Valentinia* and the two mycetophagous flies, are frequently found there. The moth larva usually completes development in the parenchyma, especially when it has entered a nut vacated by two weevil larvae, with the subsequent destruction of the whole embryo.

The two dipterans *Sciara* and *Chymomyza* are to be found in the moist, well-decayed parenchyma with the cheese mites. These, as do most of the arthropods, reduce the tissues to feces.

It is noteworthy that succession in the parenchyma is substantially the reverse of that in the embryo. In the latter the "*Chymomyza* Group" precedes the "*Tullbergia* Group" (see Fig. 2). The difference is due to the substrates; the parenchyma is hard and must be softened, while the embryo is soft and later becomes harder. In the dryest acorns, small populations of mycetophagous mites such as *Eupodes* sp. and *Tarsonemus simplex* are evident. This condition was more evident in nuts kept in the laboratory, which became too dry to support individuals of the "*Tullbergia* Group." It was not determined whether the low numbers of the former mites in moist nuts is due to competition or to habitat preferences.

The central mass is further softened by fungi and reduced to feces, sometimes repeatedly, during stage III. The slowest decay is in the lepidopteran feces which are not completely broken down after a year in the laboratory under optimum conditions. The fiber layer and testa are usually well softened by the end of this stage and may then be considered part of the central mass.

Two species of the genus *Belba,* the most common of the oribatoid mites, show a considerable rise in numbers during late stage III. The reproductive potential of these species is much lower than that of the cheese mites and collembolans; the oribatoids never reach the numbers shown by the other microarthropods. In nuts isolated in the laboratory, it took three to five months for populations to reach one hundred or more, even without predation. These small, brown mites feed on all the parts of the nuts which are firm, but softening on the surface, including the outside of the sclerotic layer.

During stage III, the activities of cellulose- and lignin-destroying fungi become evident, though extensive softening of the sclerotic layer does not usually take place until stage IV is reached. Two groups of these fungi carry out decay in different ways. The first, termed "Rapid Breakdown," is typified by *Armillaria mellia,* the oak fungus. Tough, white superficial mycelia spread indiscriminately over twigs, leaves and acorns, binding them together. All acorn tissues are softened and bleached, though there is little reduction in thickness. The latter is apparently due to the unpalatability of the mycelia and invaded tissues; there were only four records of animals feeding on these materials, even in nuts isolated in the laboratory for two years.

Within a year after invasion by *Armillaria,* acorns were softened so much that slight pressure collapsed the seemingly intact shell which could then be rubbed to a powder between the fingers.

Three to four times as many acorns as in "Rapid Breakdown" go through what has been termed "Slow Breakdown" under the influence of cellulose destroying fungi typified by *Chaetomium elatum* and *Memnoniella echinata.* The mycelia of these forms grow in the tissues rather than on the surfaces and little is evident on the surface except fruiting bodies. These and the softened surface layers are eaten by some of the mites and Collembola, especially *Tullbergia* and *Belba.* Thus the parenchyma and sclerotic layers become gradually thinner, though they remain brittle, until slight pressure is sufficient to break the shell. Nuts going through "Slow Breakdown" support much larger populations of animals and non-cellulose decomposing fungi, possibly because of some sort of antagonistic substances produced by the *Armillaria* group.

Waksman (1944) and Cummings (1954) found that *Chaetomium globosum* inhibited the growth of bacteria and many fungi, but there was little evidence for this by *C. elatum* or *Memnoniella echinata* as far as other fungi were concerned. There was always a very low percentage of bacteria evident even on the agar slants, which may have been due to inhibition.

STAGE IV

The later changes described above which are brought about by the cellulose-decomposing fungi take place during stage IV. There is little or no animal activity during "Rapid Breakdown" until the mycelia have used up all the available food and have begun to decay themselves, by which time the nut is at the beginning of the mounding stage.

During "Slow Breakdown," the increasing fragility of the shells makes for the appearance of holes, large and small, in addition to the exit holes of the large larvae. The earliest of these appears in the base of the nut when the "hilum" falls out after the softer tissues around it have decayed. This considerably reduces the protection provided in the central cavity and allows the entrance of larger animals. The amount of soil within the cavity is increased, which makes the lower portions of the shell a part of the general decaying matter of the soil. By this time, nuts are resting on the soil and the parts which are buried in it decay much more rapidly than those above the surface, even when they are under a heavy layer of leaves.

During early stage IV the central cavity is invaded by many of the animals more typical of the general floor fauna, such as centipedes, isopods, earthworms, enchytraeids, the larger Collembola, and others. Ten nuts were found which housed complete colonies of the ant, *Myrmecina americana.* Adults, pupae, larvae, and eggs were all present in relatively large numbers for the space occupied. These seed-eating ants (Wheeler 1910) contribute nothing to breakdown of the acorns, except cutting down the animal populations in the cavity and possibly removing some of the particulate matter. The populations of mites and Collembola in the parenchyma were always normal for nuts of this stage, and decay of this and the sclerotic layer went on as usual. Interestingly, a large mite of the family Parasitidae was found with most of the ant colonies and nowhere else, but evidence of predation was lacking.

It is possible that other animals use nuts in this stage as a resting place, but few were found by the method of collecting. Perhaps if the nuts were put in individual containers when collected and also taken at night, some small arthropods would be found to be using these "caves" temporarily.

STAGE V

During this period, the greatly softened shell gradually loses its identity, collapsing into a mound which is then gradually incorporated into the humus of the soil. In the few observations made on nuts of this stage, the castings of earthworms and isopods were in and on the mounds, indicating the possible role of these animals in the final breakdown.

FOOD RELATIONSHIPS

Determining the food relationshps of the animals in this study depended primarily on observation, with some simple tests where possible. The relationships determined in this study are summarized in Figure 3 for the animals and Figure 4 for the fungi and the animals feeding on them. The information in the latter is, of necessity, not as complete as might be desired. In all cases of predation listed, the author has preserved both predator and prey; the cultures in the vials proved invaluable for obtaining predation records. For the herbivores, ingestion of the fruiting bodies of fungi or of the substrate under them was construed as sufficent evidence of feeding. Many of the animals listed occurred too infrequently to be included in the discussion above, but it seemed advisable to include feeding records of these forms. Nematodes were present on all wet surfaces, but the influence and feeding habits of these very small animals were not determined.

The most important predator was found to be *Gamasellus* sp., an extremely flattened mite which is the only one capable of following the smaller mites and collembolans into the cracks and crevices. These mites were frequently found in disproportionately large numbers, 25 to 60 percent of the number of possible prey animals, though in most nuts the predator-prey ratios were more nearly what would be expected. The large numbers were usually in stage II or early stage III nuts and probably represented invasion and subsequent decimation of the prey populations. Such a condition was found for vertebrates by McCabe and Blanchard (1950). Usually this predator does not completely reduce the populations of other animals, maintaining a good balance between its numbers and the food supply. One species of the genus *Parasitus* was the only other predator found at all frequently. It was impossible to determine the importance of the larger, infrequent predators, such as centipedes, except for the pseudoscorpion *Microbesium confusum,* which reduces the animal populations to nothing in nuts that it occupies.

Feeding of the initial animals has been discussed under stages I and II, and there was little difficulty in delimiting their food. However, separating, if this is necessary, the mycetophages and scavengers (Brues 1946) was much more difficult and, in most cases, impossible. Certain of the Acarina, such as the cheese mites, are known to be primarily mycetophagous (Baumberger 1919) and they were observed feeding on pure colonies of bacteria and fungi. These forms will ingest the substrate when it is very soft, but how much of it is utilized is still not known. *Tullbergia,* the most important collembolan, and, to a lesser extent, the oribatoid mites, habitually ingest the substrate, including the agar of culture slants. This indicates strongly that these forms, at least, do utilize some of the substrate materials. The problem of food requirements of these microarthropods is being pursued even in the face of such evidence as the feeding of the

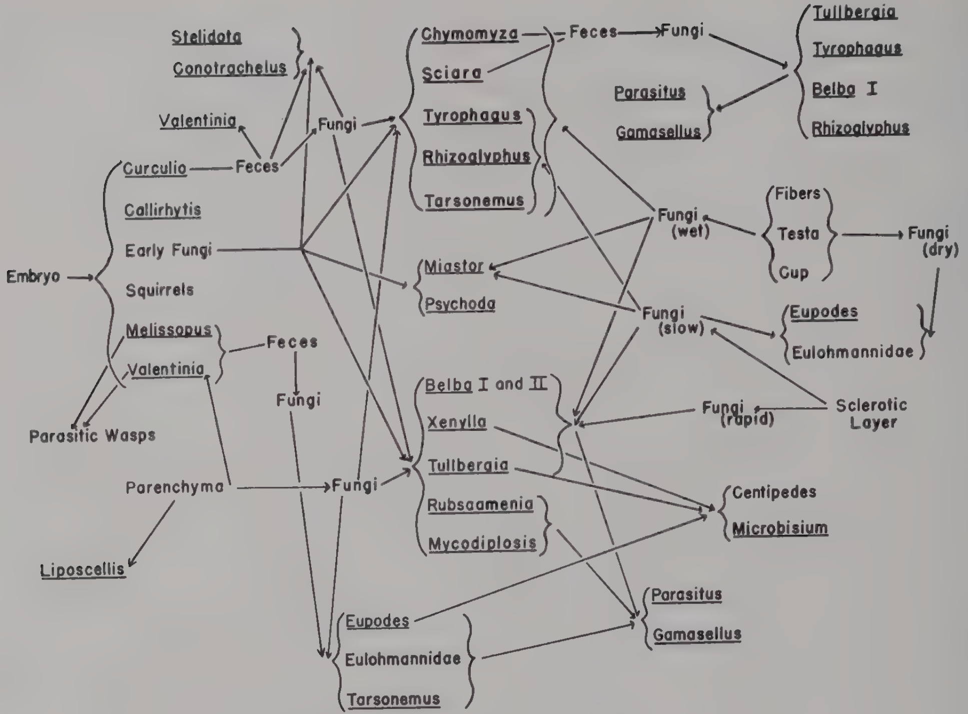

FIG. 3. Food web of animals contributing to decay with known predators and parasites.

cheese mites on the glass marking pencil used to number the culture vials.

LENGTH OF THE PERIOD OF DECAY

An attempt was made to set up criteria for the determination of the length of time the acorns had been on the ground and thus to judge the period of decay. However, no accurate methods were found because of the radical changes which take place in the tissues and the great variation in the rates of these changes. Savely (1939) found that he was unable to determine the length of time a log had been on the ground for more than three or four years without the cutting date. In the same way, there is no difficulty in distinguishing newly fallen nuts from others by general appearance and color, but beyond this, it is impossible to be certain.

The length of the period of decay of a nut depends on the conditions under which it lies on the forest floor and the organisms which have been associated with it during the entire time. Acorns in which early decay has been due entirely to fungi may be in stage II and III for a much longer time than those in which animals have contributed to breakdown of the tissues. The species of cellulose-decomposing fungi which become established influence the later stages considerably, as has been shown.

The physical conditions, acting upon the nut and its biota, largely control the length of the period. Those nuts which are covered by a layer of leaves soon after they drop remain moist and protected, constantly under optimum conditions for decay; the rate of breakdown is probably near maximal. Other acorns fall on open ground on which the leaf cover is blown off; these are exposed to drying winds and extremes of temperature. Decay in these acorns is much slower.

For most nuts, stages II and III are completed within the first year to year and a half. Those collected in the Fall can be placed in three poorly defined groups which aid in calculations of the length of the early periods of decay. The two most distinct groups are the newly fallen acorns and those in early stage III in which the parenchyma is partially destroyed and the shell is slightly softened so that it may be opened by hand but with difficulty. Because there are virtually no stage II nuts left from the previous year's drop, there is a gap which separates these two groups. All other nuts fall into a third much less well-

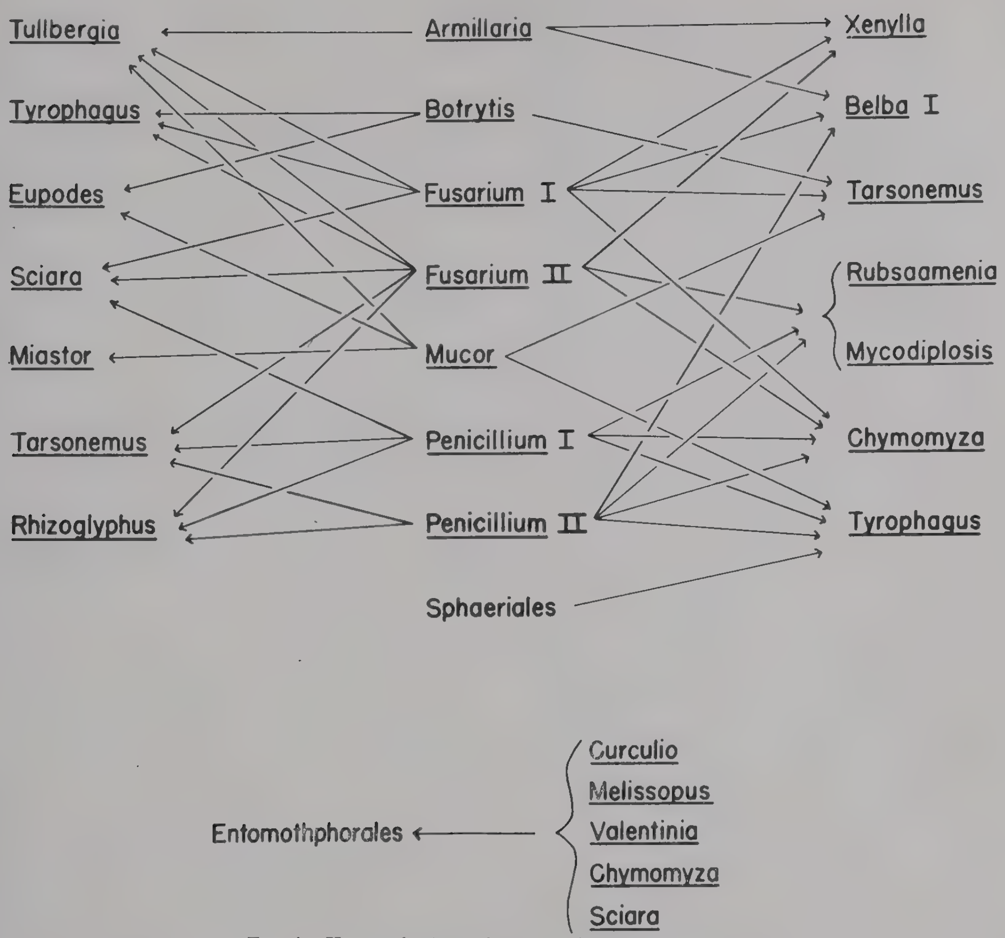

FIG. 4. Known food relationships of fungi and animals.

defined group which contains those that fell two or more years before; there is no accurate way to separate them further.

Early stage IV nuts in "Slow Breakdown" kept in vials for one year showed changes which indicate that this stage lasts for three or more years. Reduction of the parenchyma was considerable, but the softening of the sclerotic layer was far from enough to bring these into stage V. The thickness of the shell of four of these nuts was measured at the beginning and end of the period. Relatively pure cultures of *Tullbergia, Rhizoglyphus,* or *Belba* were maintained on each nut, uncontaminated by predaceous animals. The average loss of shell material was 1.1 mm on shells that averaged 2.2 mm at the start; about half the remainder consisted of the sclerotic layer which was reduced no more than 0.2 mm. In another test, two cups were kept for one year with pure cultures of *Belba.* The surfaces had been reduced about one millimeter by the action of the mites on the mold-softened tissues, at which rate these cups would not be completely reduced for five to seven years. However, indications point toward more rapid decay on the forest floor because of the feeding of other animals.

As the name implies, decay is completed much sooner under "Rapid Breakdown." Nuts may be attacked in early stage III and all the tissues are soon covered. The presence of *Valentinia,* the scavenger moth larva, in some nuts in which the shell was well-softened indicates the early invasion by *Armillaria.* Five nuts in stage III and five in early IV were kept in vials for one year. The first were definitely in stage IV by the end of this period and the shells very soft. The second group had progressed to late IV and early V and all would have been definitely mounding within the next year or two on the forest floor.

From the preceding discussion it can be seen that no accurate method was discovered by which the length of the period of decay could be determined, after the first two to three years. The variables are so numerous that it is impossible to do more than generalize. Nuts passing through "Slow Breakdown" are probably completely decayed in from four to six years with at least two years each in stages III and IV. The "Rapid Breakdown" produced by *Armillaria mellea* may be complete in two to three years from the time the nut has dropped to the ground. There is no way to set up categories for this latter process, as all tissues are attacked at the same time and the microsere is telescoped.

Discussion

Despite its small size, the acorn presents a fascinatingly complex habitat in which the life histories and relationships of many organisms may be studied. This preliminary work has served to open many more new problems than it has solved, which is as it should be. The succession in the decay of these nuts depends on a complex of organisms the activities of which take the nut through the changes which have been described. Decay is initiated by one of several possible organisms; but as the process goes on, fewer different species-types are found to be responsible, until in the late stages only a small number of significant organisms is present. In the same way, the several initial pathways of decay all lead eventually to the same end, mounding (cf. fig. 2).

The successive changes brought about by decay make it possible to set up stages arbitrarily which roughly delimit periods in the succession. The fact that there are successive changes depends on the differential resistance of the various tissues to decay and breakdown.

Succession here is as definite as in larger seral complexes; the breakdown follows a definite, though plastic, pattern when one considers only the changes in the various tissues of the nut and the species-types of the organisms important in the process and not the many possible deviations from the general scheme. These species-types may be considered in five general groups: the initial organisms, the "*Chymomyza* Group" (cf. fig. 2), the "*Tullbergia* Group," the cellulose-decomposing fungi, and soil organisms typical of stage V.

Other than setting up these groups, there was little of significance found in listing counts of animals because the small size of the acorn allows for relatively great variation in numbers and species. The listing of average populations and species makeup was considered useless, even for the several thousand nuts examined, because of these variations. In nuts in the same part of stage III, may be found any combination of four or more species of mites, two of Collembola, several fly larvae, beetle larvae, and/or *Valentinia*, with some or almost all present or absent. The forms presented in the description of the stages are those which appeared most frequently, but a glance at the faunal list will show that many more were found. Of these, *Eupodes* sp. and *Tarsonemus simplex* are two mites present many times, especially in drier nuts, but these mycetophages were found to have little direct influence on decay. This variation in species depends first on the strength of the initial invasion by each species and on the conditions for reproduction after that.

The great variation present in the acorns makes it difficult to designate those which can serve as successional indexes (Allee *et al.* 1949), but again, species-types can be used successfully for this: stage II, the itonidid larvae and the initial organisms; stage III, *Valentinia* and the "*Chymomyza* Group"; stage IV, the cellulose-decomposing fungi and the "*Tullbergia* Group"; stage V, typical soil animals.

One of the major phases of the concept of succession which is well shown here is that of change of the substrate brought about by the organisms themselves. It was found that the animals moved out of one area into another when food was exhausted or the substrate changed in some other way. The depletion of food seems to be the primary reason for migration in nuts which do not dry; this causes marked population fluctuation in some cases, especially in those mites which feed only on the aerial growth of the fungi. After this food is eaten down to the substrate, numbers are drastically reduced; after it grows up again the numbers of mites increased. In one case, this was observed for four successive cycles with one of the cheese mites and *Penicillium* I.

In those species which feed, as well, on the softened substrate, population numbers are somewhat more stable but are dependent on the rate of softening by fungal activity. In most nuts there is a rather rapid increase in numbers of the smaller forms and then a gradual decline as the food supplies are exhausted; other factors are not so important. The succession of animals can be induced by allowing nuts to dry very slowly in the laboratory so that reduced food supply comes about with reduced decay. The microarthropods become dominant in the following order: the cheese mites, *Tullbergia* and *Belba, Xenylla* and *Tarsonemus simplex,* and, last, *Eupodes.* Other tests showed these species to be tolerant to drying in this order and that moisture is one of the major limiting factors on most of them, if not the factor of greatest importance.

The insects, other than Collembola, are not affected by changes in the substrate for their life cycles are such that a change in substrate is met by a change in the life cycle, either by pupation or in feeding habits.

A further aspect of succession is that the initial organisms responsible are all quite specialized for feeding in acorns, while the later forms are less so and grade into the generalized soil animals such as earthworms. The mites, fly larvae, and collembolans feed in other similar habitats, but are not found in any numbers in the litter of the floor. *Gamasselus* was found nowhere but in the acorns and is evidently a predator somewhat specialized for this niche. *Parasitus,* a larger and less depressed predaceous mite, is present commonly in samples of the forest floor.

Seasonal succession depends on the annual drop of the acorns in the Fall, coincident with which are the life cycles of the insects, though the fly larvae are little restricted by this. Of course, the low temperatures of winter slow activity considerably, but the microarthropods, molds, and nematodes in nuts collected under the snow were somewhat active even when kept at 4° C in the refrigerator. Thus winter slows, but does not stop, the activities of the smaller organisms.

The most important agents of decay, except for the initial animals which destroy the embryo, are the fungi which change and soften the hard plant tissues but do not change the shape or identity of the shell. It is the animals which break these softened tissues down into feces and speed up the conversion of the plant materials to humus. Breakdown, as opposed to decay, is much slower when fungi are the sole agents.

The fact that conditions for survival of the initial organisms and for decay are maximal in Carlé Woods is probably the reason that less than one percent of the acorns survive to sprout. Korstian (1927) and others list survival percentages many times higher than this in stands of the more economically valuable oaks. Even though these were higher, drier sites and made up of different species, the same genera of insects and fungi were found to be initially responsible for breakdown. Cursory examination of the upland stands of white and black oaks near Evanston indicated a higher percentage of survival than in Carlé Woods. In the nearly saturated conditions prevailing under the leaves in Carlé Woods, nuts in stage I are much more liable to infestation by fungi and subsequent decay than those in the drier forests. These conditions would logically make for more rapid decay, but a comparative study with this in mind was not made.

In the study of succession in communities such as Carlé Woods, Braun (1950) and others have shown that the climax tree of flood-plain forests in northern Illinois is the sugar maple, preceded by red oaks. The physical and biotic conditions prevailing in this rich, moist habitat provide optimum conditions for the organisms that initiate decay of the acorns. This accounts for the extremely low survival of the nuts which is undoubtedly a major factor in the change from one species to another. The failure of young trees of one seral stage to grow in the shade of the adults of the next stage has been given as a primary reason for this succession (Allee *et al.* 1949), but it is possible that the small number of viable nuts surviving until Spring is just as important.

SUMMARY

1. Acorns of the red oak, *Quercus rubra,* from Carlé Woods, Des Plaines, Illinois were collected in all stages of decay for one year. These were examined for the animals and fungi present, both qualitatively and quantitatively, though the great variation in numbers precluded any but the broadest quantitative analysis. This work is an attempt to work out the interrelationships of the plants and animals inhabiting these nuts.

2. A definite succession of decay was established which could be divided into five stages, roughly delimited by certain of the animals and fungi.

3. Decay is initiated in several ways and follows numerous possible pathways (cf. Fig. 2) which anastomose and are reduced in number until a single pathway in the final stage leads to mounding and conversion to humus.

4. Known food relationships are given for the animals and a check-list of all organisms is included.

5. An attempt is made to set up criteria for determining the length of the period of decay, but this is unsuccessful.

6. Because of the optimum conditions for decay prevailing in this red oak-sugar maple floodplain forest, the number of acorns which survive is extremely low as compared with that in higher, drier sites. This is given as a possible factor in the succession from red oak to sugar maple.

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THE EFFECT OF SOME SITE FACTORS ON THE ABUNDANCE OF *HYPOMOLYX PICEUS* (COLEOPTERA: CURCULIONIDAE)[1]

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Introduction

Although *Hypomolyx piceus* (De G.) is probably indigenous to the northern forest zone of North America, it has only recently received intensive examination. This investigation was prompted by officers of the Forest Pathology Laboratory, Canada Department of Agriculture, Saskatoon, Saskatchewan, who suspected that root wounds caused by the larvae of this insect might serve as points of entry for diseases of white spruce, *Picea glauca* (Moench) Voss.

The taxonomic status of the insect is complicated by the possible existence of a species complex. This is being investigated.

H. piceus has a two year life cycle, part of two seasons being spent in the larval stage. There is extensive overlapping of the various stages and the time spent in any particular instar differs, depending on the season of its occurrence.

The adults (Fig. 1) feed on the bark of small roots and twigs and on the needles of the host, but the most serious damage is caused by the larvae (Fig. 2). The larvae bore into the bark and along the cambium of roots and root collars of the host. This damage sometimes causes death from mechanical injury or leaves lesions for the entrance of wood-rotting fungi (Warren and Whitney 1951; Whitney 1952).

This insect has been recorded attacking pines, spruces, and tamarack but most of the investigation reported here was made on white spruce. No evidence of *H. piceus* attack has been found on balsam fir, *Abies balsamea* (L.) Mill., although

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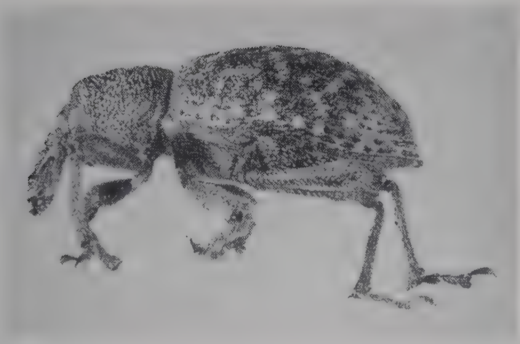


Fig. 1. *Hypomolyx piceus* (De G.) Adult (X4.5).

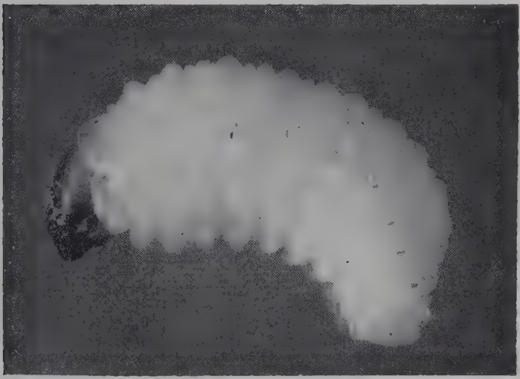


Fig. 2. *Hypomolyx piceus* (De G.). Last instar larva (X4.5).

this tree is commonly interspersed with white spruce.

Nature of Injury

The newly hatched larvae bore into the bark of the root system of the host. This boring causes resinosis, producing noticeable exudations (Fig. 3a) similar to the "pitch tubes" formed by scolytids. Using the exudation, a feeding larva forms a tube-like covering. This covering increases in size and hardness as the larva grows (Fig. 3b and 3c). A number of mature larvae, feeding close together, usually cause a copious resin flow and a solid mass of hardened tubes (Fig. 3c).

Boring larvae may be found either on roots or root collars of the host but they appear to prefer root crotches. Small trees may be completely girdled at the root collar or many of the roots may be girdled, especially at the crotches. Large trees are seldom girdled at the collar but their main roots may be girdled or severely debarked at or adjacent to crotches. Other parts of the roots are attacked but damage is usually concentrated at the positions described (Fig. 3d).

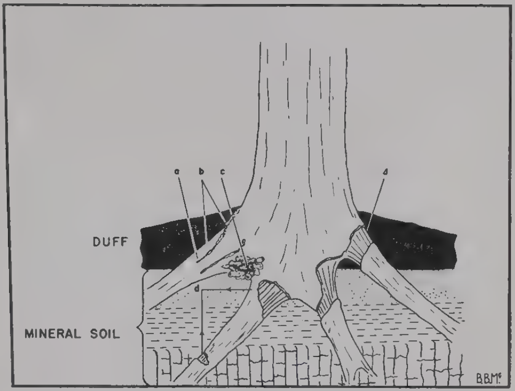


Fig. 3. Diagrammatic illustration of larval tunnels and larval damage. a, early instar larval pitch exudation; b, late stage larval tunnels advancing toward root collar; c, mass of larval tunnels and pupal cells at a root crotch; d, larval damage.

A root is considered susceptible to attack when it is more than one inch in diameter at the base. Observations indicate that where the larger roots of a tree are four or five inches in diameter at the base, the distal portions less than two inches in diameter are seldom damaged. Roots smaller than two inches, on a large tree, are usually free from attack. However, some saplings as small as one inch in diameter, at a one-foot stump, are occasionally attacked (Warren 1953).

If a tree is completely girdled at the root collar, or if the majority of the roots are girdled, the tree will die. Little mortality has been found in the areas examined in the Prairie Provinces, but severely damaged trees were frequently encountered under certain site conditions (Whitney and van Groenewoud 1952; van Groenewoud 1953). Daviault (1949) reported extensive mortality in Scots pine, *Pinus sylvestris* L., and red pine, *Pinus resinosa* Ait., plantations in Quebec.

Damage Index

Observations indicate that *H. piceus* populations differ widely in various site types. Therefore it is necessary to have some system of making population estimates for site assessment studies.

Estimates of current populations are extremely difficult to obtain because of the subterranean and subcortical habits of the insect. In addition, since damage is cumulative, yearly population fluctuations could mask the long-term relations of the insect. For these reasons, the assessment of insect abundance was based on the accumulated damage to the host trees under similar conditions in a given location. A method of rating damage, shown in Table I, was established on this basis in 1952 and has been modified as experience directed.

These ratings are subject to observational error

Table I. Classification of damage to conifer roots by the larvae of *H. piceus*

Rating	Description
0	No damage
1	A few scars, none penetrating to the cambium layer
2	Less than one-quarter of the roots girdled or killed or less than one-quarter of the surface of the root collar girdled to the cambium, or any combination of the two forms of injury being less than one-quarter in total root system damaged
3	One-quarter to one-half as above
4	One-half to three-quarters as above
5	Three-quarters to complete girdling of roots and/or root collar

but the divisions are broad enough to obtain assessments that suit the requirements. The following formula was prepared from the table so that a Damage Index could be presented in numerical terms:

$$\frac{\text{Sum of tree ratings}}{\text{Number of trees}} = \text{Damage Index}$$

Damage Index, then, represented average damage in any given area. The maximum rating possible for any tree or any area was five.

The method of rating damage was modified in 1953 to give a more detailed and accurate indication of total population for each tree. Each susceptible root and the root collar were assessed independently, using the scale from Table I. The maximum rating for each root was set arbitrarily at five. The total damage estimated for all roots of any tree was then averaged. This average was added to the assessed damage of the root collar, also having a maximum rating of five, to give a total tree rating having a maximum of ten. The Damage Index for any area was obtained by averaging results from individual trees.

The adoption of the Damage Index method was essential for population estimates, since the entire susceptible feeding area of each host had to be considered as an entity. However, if this method is used to assess the effect of *H. piceus* on tree vigor, the roots and root collar have to be assessed independently since a rating of five on either part of the root system would be fatal to the host.

SITE FACTORS

Soon after the investigation was started, it became apparent that the degree of insect damage varied between areas as well as between individual trees. Some areas escaped attack completely, while others were heavily infested with the insect. Sites with a moist, friable humus layer had a much higher Damage Index than those with a dry, hard duff. These observations indicated a need for a classification that would describe the conditions responsible for the varying levels of the insect population. In this paper site refers only to certain factors that influence the abundance of the insect rather than to the whole environment, which is the usual concept of the term.

Sites were divided into five broad moisture classes: very dry, dry, intermediate, wet, and very wet. Wilde (1940) disapproves of a similar classification used by Krudener, who classified soils as arid, dry, slightly moist, moist, and wet. Wilde contends that soil moisture varies greatly with seasons, making the terms purely empirical. This argument is valid, in the strict sense, for the classification of soils. However, the site classification used in this study is not based on soil but mainly on the type, condition, and physical and chemical properties of the humus rooting layer of conifers. Also, several other indicators were employed, all of which reflect inherent moisture conditions that are not changed by seasonal moisture fluctuations. Although admittedly empirical, the classification was adequate for the purpose intended.

Natural Indicators

In 1952, the five moisture regimes were described by using certain natural indicators: topography, flora, soil profiles, type and condition of duff, and water level. In 1953, several physical and chemical analyses were conducted on humus material collected from different site classes.

Sites have been examined at Strachan, Alberta, and in northern Saskatchewan and Manitoba, with the most intensive study concentrated at Riding Mountain National Park, Manitoba. Locations that were site-typed with relevant *H. piceus* Damage Indices will be designated throughout this text as indicated in the following tabulation:

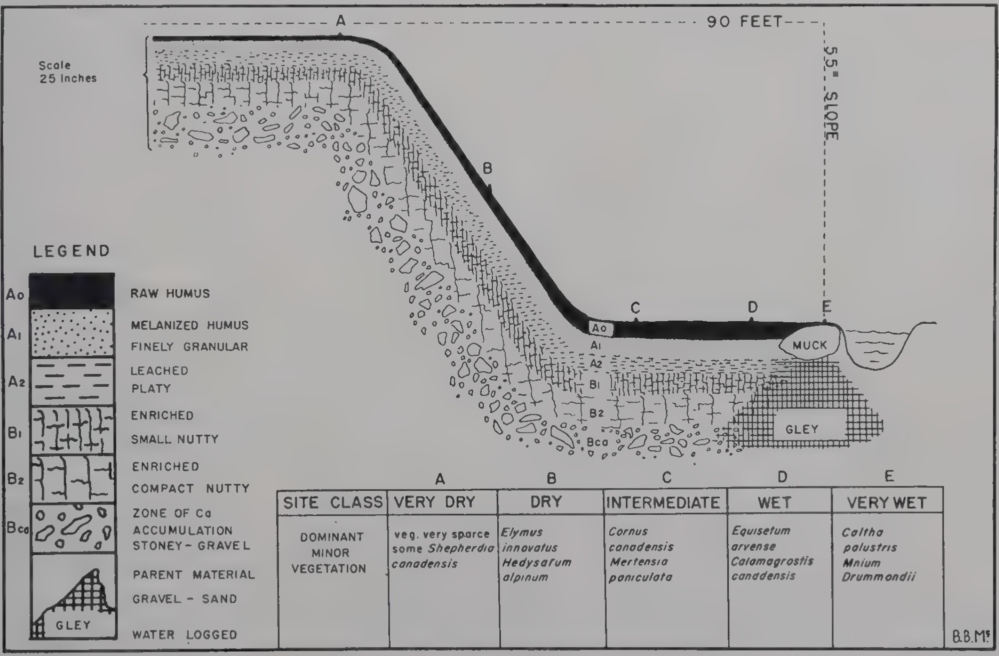
No.	Area	Location
I	Riding Mountain National Park, Manitoba	Mile 7, North Shore Road
II	Riding Mountain National Park, Manitoba	Mile 9, Norgate Road
III	Riding Mountain National Park, Manitoba	Mile 14, Dauphin Road
IV	Riding Mountain National Park, Manitoba	Mile 28, Old Strathclair Road
V	Candle Lake, Saskatchewan	Clear Sand Creek
VI	Madge Lake, Saskatchewan	Manitoba-Saskatchewan Boundary
VII	Strachan, Alberta	Provincial Warden Station

Unfortunately no one location containing the five moisture classes and a heavy infestation of *H. piceus* was available, but location I approximated such a condition. Five moisture classes were distinguishable in location I, but only a few white spruce occurred and insect damage was low. Since no better location could be discovered, Riding Mountain number I was examined in detail in 1952 and was used as a basis for establishing the classification. Later investigations in other areas indicated that all classes found in a given area fitted quite readily into the general classification and displayed comparable Damage Indices.

Location I is described in some detail to show the method of classification. It is obvious that soil profiles, flora, etc., will vary between locations as local climates vary, especially where great distances separate the areas. Figure 4 pictorially describes location I. It is situated on a steep slope terminating in a narrow valley, traversed by a brook. The soil profile was shallow and weakly podzolized at the top of the slope, progressively increasing in depth and character of profile toward the bottom. In the narrow valley a meadow soil or swamp podzol occurred with wet conditions. Figure 4 was based on information drawn from pits dug at points shown at A, B, C, D, and E. These points were selected by using the natural indicators mentioned and coincided with the five moisture classes enumerated above. In the following detailed description of location I, several examples of modifications from other areas are included for illustrative purposes. The names of all the plants listed were taken from Fernald (1950), except *Elymus innovatus* Beal. which was taken from Rydberg (1932).

Type A—Very dry. (Fig. 4A). The ground at the base of the trees was overlain with a mat of undecomposed spruce needles. These formed the bulk of the humus layer, which was shallow, compressed, felt-like, and tough. The "A_1" horizon of the mineral soil was black, shallow, and finely granular. The "A_2" was gray and weakly platy. The "B" horizon was weakly columnar and light brown to brown, not dark as in well leached soils. Investigation has shown that dense clumps of white spruce on well drained, gravelly soils are indicative of very dry *H. piceus* sites. In location I the minor vegetation of Type A consisted of arid-tolerant species which were not sufficiently abundant to break up the duff. The most common species was *Shepherdia canadensis* (L.) Nutt.

Another striking example of a very dry site was encountered in location IV. This area was an outwash plain with a shallow, northern black-earth soil profile. Prairie fires restricted the advance of the forest until recent years, and the soil climate and characteristics of a dry prairie persisted in the face of an invasion of young white spruce. A compact sod mat was present rather than the usual forest humus, and grasses predominated in the ground vegetation. Such dry-site indicators as *Festuca scabrella* Torr. and *Stipa comata* Trin.



	A	B	C	D	E
SITE CLASS	VERY DRY	DRY	INTERMEDIATE	WET	VERY WET
DOMINANT MINOR VEGETATION	veg. very sparce some *Shepherdia canadensis*	*Elymus innovatus* *Hedysarum alpinum*	*Cornus canadensis* *Mertensia paniculata*	*Equisetum arvense* *Calamagrostis canadensis*	*Caltha palustris* *Mnium Drummondii*

FIG. 4. Topography, soil profile and plant indicators depicting the five site types of location I.

and Rupr. were the most abundant species found. Here again very little minor vegetation occurred within the periphery of the dense coniferous growth and the humus was a tightly packed, raw needle layer. *H. piceus* was entirely absent from this area.

Type B—Dry. (Fig. 4B). The humus layer under the trees was similar to that in A position but more minor vegetation occurred and some fungal mycelia were apparent. These two features made the duff more porous and friable. Topographically, B was situated about halfway down the slope. The soil profile resembled that of position A but was slightly deeper. The most common herbaceous plants were *Elymus innovatus* Beal., *Hedysarum alpinum* L., and *Agastache Foeniculum* (Pursh) Ktze.

Type C—Intermediate. (Fig. 4C). The humus layer was deep, mellow, friable, and considerably decomposed. A prominent mat of fungal mycelia indicated increased micro-organic activity. This activity, together with an abundance of minor vegetation, served to break up the duff. Higher moisture content was indicated by the increased micro-organic activity and the presence of more mesic plant species. The most abundant species were *Cornus canadensis* L., *Mertensia paniculata* (Ait.), *Aralia nudicaulis* L., and *Petasites palmatus* (Ait.). The intermediate site is the most common in all areas examined and usually occurs in mixed aspen, *Populus tremuloides* Michx., and white spruce stands. It does not necessarily assume a topographic position as shown in Fig. 4C but is similar in other indicators.

Type D—Wet. (Fig. 4D). The humus layer was mossy and spongy. The soil was a hydromorphic meadow podzol with a gley horizon extending to the top of the "B" horizon. The minor vegetation was abundant, especially mosses. The most common plants were *Calamagrostis canadensis* (Michx.) Nutt., *Mitella nuda* L., *Equisetum arvense* L., and *Mnium* spp. Water was not found standing at root level but water marks on the roots indicated flooding during wet spring and fall seasons. Wet sites in other areas were of two types. The first had an uneven surface with trees standing on the hummocks, their roots extending into depressions that act as temporary reservoirs. The second was a level bog-fringe stand, having a permanently high water table with the trees growing just above the summer water level.

Type E—Very wet. (Fig. 4E). The humus layer consisted of newly formed peat, deeper than in the wet site. It was spongy when wet and friable when dry. The marsh-marigold, *Caltha palustris* L., predominated the minor vegetation. The soil was a swamp podzol or bog type, with the gley horizon extending into a mucky "A" horizon. Water was found at root level, even in mid-summer. Extensive white spruce stands do not occur in sites of this type but a similar condition was found in another white spruce stand in Riding Mountain during 1954. It contained the highest active population of *H. piceus* ever encountered by the author.

HUMUS ANALYSIS

Humus was analysed to establish measurable characteristics by which more precise site comparisons could be made. The characteristics measured were: field moisture, bulk density, pore space, moisture equivalent, and loss on ignition. Three samples were drawn from around the base of each sample tree in location V and two from each tree in locations I and VI. The trees within the locations were chosen by site, using natural indicators. Samples were collected in tins having a capacity of 623 cc., using a modification of the method described by Leisman (1953). The humus mat was collected down to the mineral soil.

The two tests that produced the most acceptable ranges through the site classes, and that were significantly related to the *H. piceus* Damage Index, were moisture equivalent and loss on ignition. The only economically feasible method for determining moisture equivalent was that of Bouyoucos (1929). This method utilizes a Buechner funnel and water suction pump. Loss on ignition was obtained by burning finely divided, air-dried soil to constant weight at 600° C. in a muffle oven. The results obtained compared favorably with a number of samples tested by the more cumbersome chromic acid method.

SITE FACTORS AND DAMAGE RELATIONSHIP

Since the original method of calculating Damage Indices was modified in 1953 it is necessary to discuss the results of the two years' investigations separately.

Table II is an analysis of data collected in 1952 at Riding Mountain National Park and in 1953 from other areas. Natural indicators were used in both years for determining site type but the revised system for assessing damage was used for 1953.

The same trends are apparent in both years. Regardless of methods used to assess damage, or locations from which data were collected, the incidence of *H. piceus* damage increases from dry to wet sites. Both years illustrate that a regular progression, approaching a direct proportion, exists between Damage Indices and moisture classes within locations. With one exception, the

TABLE II. Damage Indices with relation to moisture classes

Year	Location	Moisture classes (Numbers of trees in brackets)				
		A	B	C	D	E
1952 Maximum Damage Index=5	I	0.8 (20)	1.7 (20)	2.5 (20)	3.7 (10)	3.6 (10)
	II	....	1.5 (10)	2.3 (10)	3.8 (10)	
	III	....	1.5 (8)	2.6 (12)		
	IV	0.0 (20)				
1953 Maximum Damage Index=10	V	....	0.6 (10)	3.1 (10)	3.9 (10)	
	VI	....	0.3 (11)	3.0 (11)		

"F" values, calculated from the analysis of variance for testing the differences in Damage Index between moisture classes, exceed the one per cent level of significance (Table III). Location III is significant at the five per cent level. This location is composed of dump till and it is very difficult to sort trees by groups in such a heterogeneous site. The results from the years 1952 and 1953, shown in Table II, cannot be directly compared because of the differences in sampling techniques, but the same trends are apparent. As was expected, considerable variation in Damage Indices occurred between widely separated areas, since local populations of the insect differ.

TABLE III. Analysis of variance for testing differences in Damage Index between moisture classes

Location	Degrees of freedom		Error mean square	F value
	Moisture class	Error		
I........	4	75	1.10	19.85
II........	2	27	1.12	12.17
III........	1	18	1.01	7.43*
IV........	No *H. piceus* damage.			
V........	2	27	2.37	12.75
VI........	1	20	3.11	13.77

*Significant at the 5 per cent level; all others significant above the 1 per cent level.

Tables IV and V show the results of the humus analyses of the material collected from individual trees in 1953. The analysis of variance for testing the significance of the linear regression between *H. piceus* Damage Index and moisture equivalent, calculated from ungrouped data, follows:

Source	*Degrees of freedom*	*Mean square*	*Calculated F. value*	$F_{.001}$
Due to regression	1	74.54	25.10	approx. 11.6
Deviation from regression	100	3.01		

A similar statistical analysis was conducted to test linear regression between *H. piceus* Damage Index and loss on ignition. The data follow:

Source	*Degrees of freedom*	*Mean square*	*Calculated F. Value*	$F_{.001}$
Due to regression	1	58.87	18.57	approx. 11.6
Deviation from regression	97	3.17		

In both the above cases the "F" value obtained was significant beyond the .001 level, showing that moisture equivalent and loss on ignition are highly significant indicators of *H. piceus* site type.

Table VI shows the results of moisture equivalent and loss on ignition analyses of humus removed from over the roots of lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm. at Strachan, Alberta, in 1954. These results, although collected from a different climatic zone and from a different host, reflect the same progression of *H. piceus* damage, increasing from dry to wet sites. The higher Damage Index occurring in this area may be attributed to zonal population differences but it does not detract from the value of the system.

These two physical tests might well be visualized as tools for establishing stand hazard ratings for this insect. They might be used with natural indicators or separately. There appear to be two major advantages in using mechanical analyses of humus as *H. piceus* indicators. First, they eliminate observational errors that occur when the more subjective natural indicator method is em-

TABLE IV. Comparison of per cent moisture equivalent with Damage Index 1953

Per cent moisture equivalent	Locations			Mean Damage Index	Standard deviation (ungrouped data)	Number of samples
	I	V	VI			
80 - 105........	1.2	0.0	...	0.8	±0.37	6
106 - 131........	1.0	1.0	0.7	0.9	±0.27	17
132 - 157........	1.9	0.4	0.7	1.3	±0.32	19
158 - 183........	2.2	2.7	2.5	2.4	±0.30	38
184 - 209........	3.6	3.6	2.2	3.3	±0.54	13
210 - 235........	2.3	4.8	5.6	4.1	±0.76	6

TABLE V. Comparison of per cent loss on ignition with Damage Index 1953

Per cent loss on ignition	Locations			Mean Damage Index	Standard deviation (ungrouped data)	Number of samples
	I	V	VI			
30 - 39..........	1.4	0.0	...	0.9	±0.43	8
40 - 49..........	0.8	0.9	0.3	0.7	±0.18	11
50 - 59..........	1.8	1.2	0.5	1.4	±0.28	18
60 - 69..........	2.8	2.1	1.9	2.4	±0.43	26
70 - 79..........	2.0	2.8	4.5	2.7	±0.38	24
80 - 89..........	...	3.5	...	3.6	±0.52	12

Table VI. Comparison of per cent moisture equivalent and per cent loss on ignition with Damage Index for location VII 1954

Per cent moisture equivalent	Damage Index	Number of samples	Per cent loss on ignition	Damage Index	Number of samples
106 - 131	2.9	2	50 - 59	2.5	2
132 - 157	4.4	3	60 - 69	4.4	5
158 - 183	5.8	5	70 - 79	7.0	3

ployed. Secondly, they make it possible to classify accurately the moisture position of individual trees that occur within any one apparent site type chosen by natural indicators.

DISCUSSION

Although the data presented in this paper indicate that sites may be evaluated for *H. piceus* susceptibility, there are instances where the procedures described would have to be modified to describe existing conditions accurately. A notable example was observed when certain dry sites were examined. From the foregoing, it would be expected that the insect damage would be very low. This was true in all cases except where rotted logs were found lying buried over the roots of living trees. Almost invariably, evidence of *H. piceus* damage was found beneath the rotted logs whereas the rest of the root system might be entirely free from attack. This may be explained by the increase in the percentage of moisture content of decaying wood over that of the adjacent humus (Place 1950). Either the adult insects seek out oviposition sites in the environment best adapted to their requirements or the eggs require more moisture than is provided by humus in a dry site. These postulations have not been examined experimentally, but from field evidence the first is the more probable. It is obvious that the presence of quantities of decaying wood, in an area to be sampled for *H. piceus,* would introduce complications beyond those normally encountered in site typing for this insect.

Any soil humus characteristics, such as percentage of organic matter and friability, that are closely related to moisture holding capacity, may be used as site susceptibility indicators. However, noticeable quantities of extraneous material, such as mineral soil or rotted wood must be excluded from humus samples. Site classification may also be complicated by recent changes in ground water level. Furthermore, since sites are in a continuous state of flux, any susceptibility rating established at a given time will change as the stand age, density, and composition changes. These changes may occur through natural development or be precipitated by external forces or manipulation.

In the determination of Damage Index, the principal source of error is the failure to locate *H. piceus* damage, especially in root crotches and at low levels of insect density. Within these limitations, susceptibility of sites to *H. piceus* damage may be classified by using natural indicators and humus analysis. This classification may be valuable for intended reforestation or plantation programs.

ACKNOWLEDGMENTS

The writer is deeply indebted to his colleagues at the Forest Biology Laboratory, Winnipeg, for their advice in planning the investigation and assistance in the preparation of this paper. The writer is also grateful to Mr. J. S. Rowe of Canada Forestry Branch, Winnipeg, for his assistance in editing the site aspects of the paper and to Mr. W. E. Clark of the Canada Plant Pathology Laboratory, Winnipeg, for photographing the insect specimens.

SUMMARY

The larvae of *Hypomolyx piceus* (De G.) bore under the bark of the root systems of most conifers in the northern forest zone. This boring causes resinosis and larval damage may be traced by the resulting resin tubes. Most of the damage occurs at the root collar or in root crotches.

A method was devised to assess the cumulative *H. piceus* damage. The individual roots and the root collar of each tree were rated separately and a maximum rating of five was arbitrarily assigned to each. The individual root damage was averaged for the tree and the average added to the root-collar damage, giving a maximum rating of ten for any tree.

A Damage Index was established for each site by dividing the sum of individual tree ratings by the number of trees. Using this Damage Index, it was possible to compare relative population densities of *H. piceus* in different sites.

The degree of insect damage was related to differences in the moisture content of sites. Natural indicators and humus analysis were used to divide sites into five broad moisture classes: very dry, dry, intermediate, wet, and very wet. Two methods of humus analysis, loss on ignition and moisture equivalent, proved to be excellent indicators of the suitability of sites to *H. piceus* attack.

The site evaluation technique would require modification where obvious amounts of extraneous material, such as rotted logs, occur in any particular site or where ground water levels have recently changed.

Analysis of data showed that insect damage was more common on wet sites than dry ones.

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SOME OBSERVATIONS IN A TROPICAL RAIN FOREST IN CHIAPAS, MEXICO

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INTRODUCTION

Though there has been an increasing interest in the fauna and flora of the rain forests of the neotropical region, only a few studies have been made in which an analysis of the entire community has been attempted. Studies of individual groups of animals have contributed much to our knowledge of tropical ecology; however, it is only by investigations of the entire community that foundations can be laid for an understanding of the coactions and reactions of the complex plant and animal relations.

One of the most comprehensive surveys of the animals of a tropical rain forest was Allee's (1926) on Barro Colorado Island. This thorough study included not only observations on animals, but also physical factors and their effect upon animal distribution. Williams (1941) did a survey of the floor fauna of Barro Colorado Island in which he analyzed the occurrence and density of the various inhabitants. He also correlated this distribution with environmental factors. An earlier study by Beebe (1916) consisted of a careful listing of the animals found in a square foot of forest soil and debris from a Brazilian rain forest. The latest study of this type is that of Strickland (1945) in Trinidad. He surveyed the arthropod soil and litter fauna of forest and cacao plantations.

For the rain forests of the Old World, some of the most important work is that of Dammerman (1925 and 1937). In his work he listed quantitatively the fauna found in tropical soils and surface litter in Krakatau Islands and Sumatra. Handicapped though he was by the difficulty of getting proper identifications, his work is of significance. Corbet (1935) summarized his observations in Malaysia on the influence of the soil fauna on fertility.

The study reported here was undertaken during the summer of 1949 when we had the opportunity of spending the entire month of July in the undisturbed rain forest surrounding the archeological site near Palenque, Chiapas, Mexico. Since so few studies have been made on the animal ecology of the rain forest and none at all in Mexico, it is believed that these studies will contribute to our understanding of tropical ecology. Throughout this study we have been faced with the same problems that all other investigators have had, namely, that of getting identifications of the invertebrates. A study of this type impresses one with the great need for more comprehensive investigations into the taxonomy and life histories of the tropical forms. In spite of these limitations, it is hoped that studies such as these will at least outline the problems and needs of future work in similar areas.

Acknowledgments

As is to be expected from a study such as this, there are many scientists whose help was invaluable. Dr. Milton Sanderson of the Illinois Nat-

ural History Survey spent many hours sorting the beetles to families and identifying the Staphylinidae and members of the genus *Phyllophaga.*

Other individuals who identified various groups are as follows: Dr. José Alvarez (fish), Dr. E. W. Baker (mites), Dr. H. B. Baker (mollusks), E. C. Becker (Elateridae), Dr. L. Belkin (Bostrichidae), Dr. W. M. L. Brown, Jr. (ants), Dr. F. A. Chace, Jr. (crabs), Dr.. R. Crabill (Chilopoda), Dr. P. J. Darlington, Jr. (Carabidae), Dr. L. S. Dillon (Cerambycidae), Dr. A. E. Emerson (Isoptera), Dr. W. J. Gertsch (spiders), Mrs. L. Gloyd (Odonata), Dr. C. C. Hoff (Pseudoscorpionida), Dr. R. L. Hoffman (Diplopoda), Dr. I. La Rivers (Tenebrionidae), Dr. H. B. Leech (Gyrinidae), Dr. P. W. Oman (Homoptera), Dr. M. Robinson (Scarabaeidae), Dr. E. S. Ross (Embiidae), Dr. R. I. Sailer (Hemiptera), Dr. H. Smith (Amphibia and Reptilia), Dr. K. Sommerman (Psocidae), and Dr. F. Werner (Euglenids).

Permission to stay at the archeological site for this study was granted by Dr. Eduardo Noguera of the Instituto Nacional de Antropología e Historía, Mexico, D.F. and Dr. Alberto Ruz. The surveys of the mammals, birds, and reptiles were carried out respectively by our three field companions, Mr. Merle Kuns, Dr. R. E. Tashian, and Mr. W. Rockhold. Dr. V. E. Shelford of the University of Illnois must also be thanked for the encouragement and valuable advice which he gave us during the analysis of the data. This study was made possible by a special grant from the Purdue Research Foundation.

The Study Area

The forests in the vicinity of the archeological ruins of Palenque are located about five miles southwest of the town of Palenque, Chiapas. They are in the foothills of the Sierra de Palenque at an altitude of about 210 meters. The annual rainfall for the town is given as 3200 mm. The forests surrounding the ruins were undisturbed and were a typical canopied rain forest with many layers of vegetation (Fig. 1).

As is typical of the tropical forest, there were numerous species of plants, most of which we were unable to identify. Conspicuous among the trees

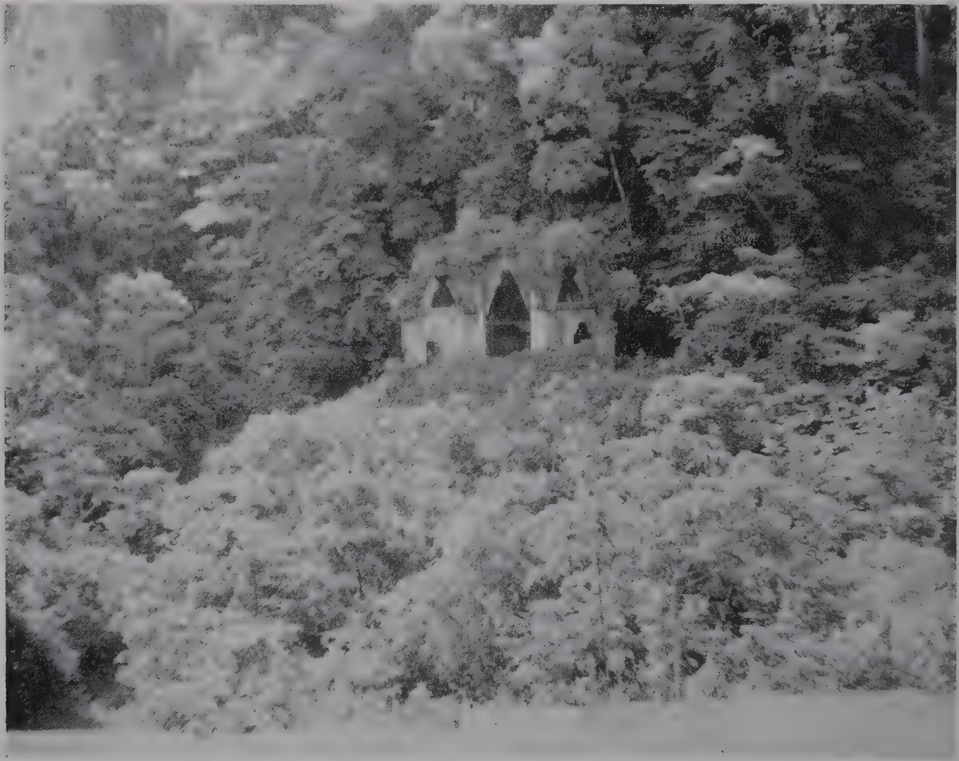

FIG. 1. General view of forest from clearing around a ruin. The foreground shows the result of clearing.

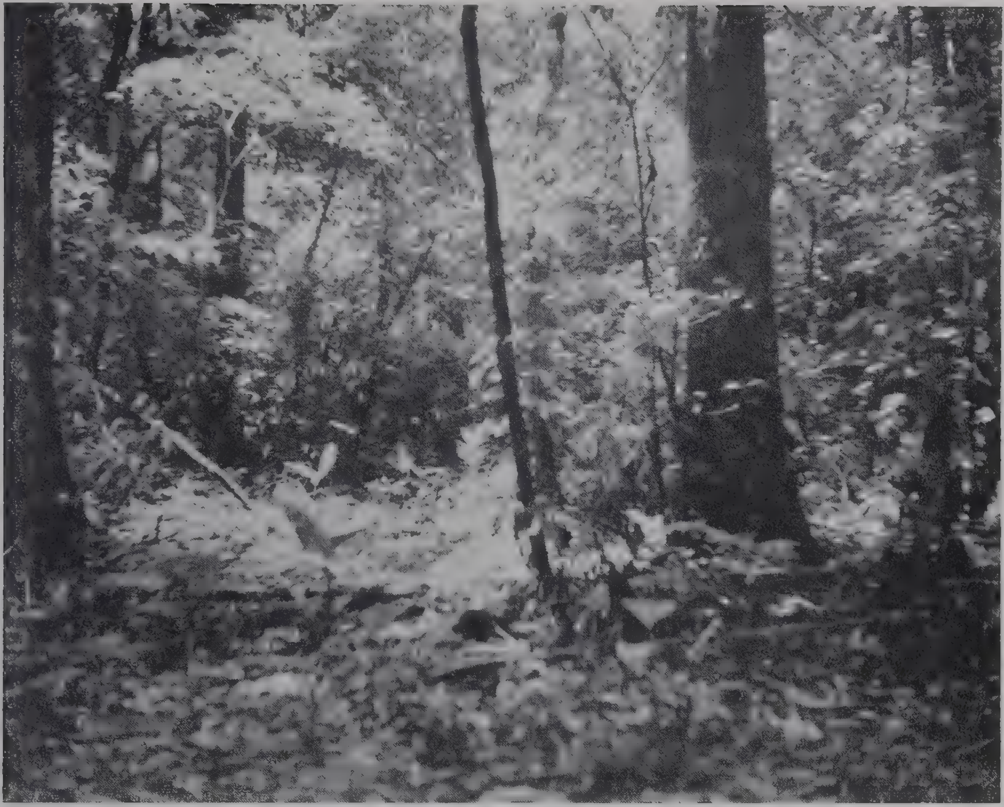

FIG. 2. View of the interior of the forest showing young trees and ground cover.

were the mahogany (*Swietenia macrophylla* King), Mexican cedar (*Cedrela mexicana* Roem.), and chicozapote or the sapodilla tree (*Achras zapota* L.). The thatch palm (*Cryosophila argentea* Bartl.) was abundant. This thorny plant made travel difficult in some areas (Fig. 2). In many regions of the forest, the surface was covered with large ferns. Except for these, there was relatively little ground herbaceous vegetation. Miranda (1952, 1953) lists other characteristic trees of the tropical rain forest of this area of Chiapas.

We estimated that the herbaceous layer covered about 60% of the ground; in disturbed areas, it covered as much as 80%. This layer was about one meter high and was mainly composed of ferns. The shrub layer (three to four meters high) consisting chiefly of the thatch palms and young trees covered 40% to 50%. The low tree layer, approximating 10 meters in height, gave 100% cover. The high tree layer, 30 to 40 meters or more in height, also gave a total cover. In these large canopy trees were many epiphytes, bromeliads, and vines.

METHODS OF STUDY

Standard ecological methods for sampling the fauna were used throughout this study. Essentially these are the methods outlined by Shelford (1951) and based on his work in the temperate zone.

The leaf litter and soil were sampled by gathering 0.1 square meter and then carefully sorting it by hand. In most cases, the material was taken out of the forest to the field station where the light was adequate for more careful observation. The herb and shrub layer (approximately one meter above the ground) was sampled by use of a beating net. In each sample, 48 sweeps was considered to represent the fauna over a square meter of soil. Unfortunately it was impossible to analyze the fauna of the upper layers of trees. These quantitative observations were supplemented by the use of field Berlese funnels and by intensive cruising under logs, in leaf litter, in termite nests, under rocks, and in other possible places.

Because of the tremendous variety of the fauna and its dispersal in the undisturbed forest, both day and night cruising proved to be one of the most valuable methods of sampling. Unfortunately such results are not quantitative.

Reptiles and amphibians were collected and observed only by cruising methods as they did not lend themselves to quantitative work. Birds, likewise, were sampled by cruising and could only be indicated as to relative abundance. Quantitative work is extremely difficult in such a forest where the smaller, less conspicuous birds may be overlooked even by the trained observer. Larger mammals such as the monkeys, cavy, and tejon were hunted by day and night. The smaller rodents were trapped by means of snap traps baited with peanut butter. Quadrat trapping was undertaken and a rough estimate was obtained. Unfortunately, many difficulties were encountered in this quantitative trapping. A sudden rain might set off the traps, and slugs, ants, and other small forms often disposed of the bait before any small mammal could get near it. Approximately 0.5 acre was trapped for three consecutive nights. This method was shown by Goodnight and Koestner (1942) to be adequate for sampling any given area. Several such quadrats were sampled.

Though we tried to sample the fauna as quantitatively as possible, we were convinced that further studies of more nearly adequate sampling methods for these forests should be undertaken. Many important animals are easily overlooked due to a lack of knowledge of their habits, or perhaps due to the fact that the season is not the proper one for their appearance.

PHYSICAL ENVIRONMENT

In addition to gathering biological data, observations were made on various climatic factors (Table I.) These studies were made during a time when the heavy rains of the rainy season were just starting. While it did not rain every day, there were occasional heavy showers. Temperature and humidity readings were taken three times a day in the clearing near the ruins. Comparable readings were taken approximately three-fourths of a mile within the forest. In this latter area, soil temperatures were also recorded. In all these observations, a laboratory-type mercury thermometer was used, and the humidity was taken by means of a sling psychrometer. The amount of light available in the different habitats was carefully measured by means of a photoelectric light meter.

The heavy vegetation of the forest strikingly reduced the amount of light on the floor of the forest. In midday when there was bright sunlight, the following readings were noted within the forest. In a clearing resulting from the felling of a

TABLE I. Climatic data, July 7-20, 1949. The data from within the forest were taken approximately three-quarters of a mile from the forest edge; those taken in the clearing were from the camp area

	Temperature, °C	Humidity, %
July 7. No rain during night.		
Clearing 8:00 A.M.	26.6	78
12:00 N.	31.1	69
4:00 P.M.	31.1	63
Forest, air 10:00 A.M.	28.5	90
soil 10:00 A.M.	26.0	
July 8. No rain during preceding night.		
Clearing 9:00 A.M.	27.2	82
12:00 N.	30.0	72
4:00 P.M.	31.6	60
Forest, air 6:00 P.M.	31.1	69
soil 6:00 P.M.	27.2	
July 9. Rain during preceding night.		
Clearing 8:00 A.M.	26.6	82
12:00 N.	31.1	58
Forest, air 7:00 A.M.	26.6	95
soil 7:00 A.M.	25.0	
July 11. Shower during night.		
Clearing 7:00 A.M.	23.3	86
12:00 N.	29.4	66
4:00 P.M.	30.1	64
7:30 P.M. (after rain)	26.1	100
July 12. Rain during night.		
Clearing 8:00 A.M.	25.0	95
12:00 N.	28.8	75
4:50 P.M.	26.6	60
Forest, air 7:30 A.M.	28.0	98
soil 7:30 A.M.	24.0	
July 14. Rain during night.		
Clearing 8:00 A.M.	25.5	100
1:30 P.M.	31.6	69
7:00 P.M.	27.2	82
Forest, air 12:00 N.	26.6	91
soil 12:00 N.	26.0	
July 15. Trace of rain during night.		
Clearing 8:30 A.M.	26.6	86
12:00 N.	32.0	69
4:00 P.M.	28.8	87
July 16. No rain during night.		
Clearing 8:00 A.M.	26.1	82
11:30 A.M.	30.0	75
4:00 P.M.	31.0	69
8:15 P.M. (during rain)	24.0	100
July 17. Rain during preceding evening.		
Clearing 8:00 A.M.	22.8	100
12:15 P.M.	29.0	83
3:45 P.M.	30.5	72
July 18. No rain during preceding night.		
Clearing 12:30 P.M.	31.0	78
5:10 P.M.	30.0	79
Forest, air 10:30 A.M.	28.8	83
soil 10:30 A.M.	25.0	

TABLE I. Continued

	Temperature, °C	Humidity, %
July 19. Trace of rain during night.		
Clearing 7:40 A.M.	23.9	90
12:00 N.	30.0	75
4:00 P.M.	32.0	63
July 20. No rain during night.		
Clearing 8:00 A.M.	29.0	95
1:00 P.M.	32.0	85
4:00 P.M.	31.6	72
Forest, air 9:30 A.M.	27.0	76

large mahogany tree, there were 3.2 foot-candles of light three feet above the ground. This reading was taken with the light meter in a horizontal position. In the undisturbed areas, under the understory ferns at a height of about one foot, 0.8 foot-candles were recorded. At three feet above the ground with the light meter pointed straight up, 1.6 foot-candles were noted. In a heavily shaded dry arroyo at four feet above the ground, only 0.2 foot-candles were detected. In contrast to these was the amount of light recorded in an area denuded of vegetation by large ants. Here we found 200 foot-candles.

SOIL AND LEAF-LITTER FAUNA

As is typical in all tropical rain forests, the bacterial action rapidly decomposes the leaf and stick litter. As a result, it was found impractical in most cases to distinguish between the fauna of the leaf litter and the soil proper. The humus layer was very thin, in most cases averaging only one to one and one-half inches in depth, and it was underlain by clay. In most areas, limestone rock was under the shallow soil and outcroppings of these rocks were present throughout the area.

Since the methods used in this study were the same as those used by Shelford and his collaborators in their studies of a temperate deciduous forest, the results can be compared. In June, 1949 the soil and leaf litter population of the deciduous forest near Urbana, Illinois averaged 1090 individuals per square meter. This total does not include mites, Collembola, or ants. To make our average of 407 individuals per square meter comparable to theirs, we must deduct these same animals. This then makes 306 individuals per square meter which is considerably below their average. Over a period of 17 years the soil and litter population of this deciduous forest averaged 714 individuals per square meter during the month of June. The lowest figure for the temperate forest was 125 during the drought period of 1934 (personal communication from V. E. Shelford). It is interesting to note that our collections also reflected the dryness of the period. For example, after one heavy rain during the night of July 11, the population took a sudden leap from 380 individuals per square meter (Table II) as noted on July 9 to 870 on July 12. Our figures thus should be considered as representative of the dry-season fauna. The rainy season appeared to be somewhat delayed in starting, and the inhabitants of the area assured us that it was an unusually dry year.

TABLE II. Analysis of soil and litter fauna collected in 0.1 square meter. The first list under July 6 represents material found in leaf litter; all others are from both soil and litter

Date: (July)	6	6	7	9	12	14	16	18
Earthworm	4	8	...	...	6	6	8	4
Gastropod (snail)	...	4	...	3	...	...	...	...
Onychophoran	...	...	...	...	1	...	...	...
Isopod (sowbug)	3	...	...	...	4	7	...	2
Acarina (mites)	2	2	1	1	2	...	...	...
Opiliones	...	...	...	...	1	...	...	...
Schizomidae	1	...	2	1	...	...	...	1
Tarantulidae	...	...	...	...	1	...	...	...
Araneae (spiders)	5	...	2	2	21	7	15	6
Diplopoda (millipedes)	5	7	...	2	13	...	3	10
Chilopoda (centipedes)	...	1	1	2	4	1	...	1
Pseudoscorpionida	2	1	...	1	3	...	...	4
Collembola	...	1	1	...	2	...	1	1
Thysanura	...	...	...	...	...	...	...	2
Orthoptera	10	1	...	...	4	...	...	...
Dermaptera	...	...	...	...	5	...	...	...
Embioptera	...	...	...	...	1	...	...	1
Thysanoptera	...	...	...	...	...	...	1	...
Coleoptera								
Cerambycidae	...	...	...	...	...	1	...	...
Coccinellidae	...	...	...	...	...	1	1	...
Scarabaeidae	...	...	...	...	...	...	1	...
Orthoperidae	...	...	...	...	...	...	1	...
Scydmaenidae	...	...	...	...	...	...	1	...
Pselaphidae	...	...	...	1	1	...	...	...
Staphylinidae	4	...	...	1	2	...	1	...
Diptera	1	...	...	...	...	...	1	...
Hymenoptera	...	...	...	...	...	1	...	...
Formicidae (ants)	15	2	8	22	9	1	10	8
Insect larvae	14	1	2	2	7	2	3	1
TOTAL	66	29	17	38	87	27	47	41

Dammerman (1925) in his work in the virgin forest of Krakatoa reported an average of about 100 individuals per square meter of soil and litter during the month of April.

Our number of indviduals per square meter is considerably lower than that given by Williams (1941) for Barro Colorado Island. It is probable that our methods were not nearly so accurate as his, and thus may account for the difference. However, in his sample, which he sorted by hand, he obtained only 294 individuals. When he used Berlese funnels, the number rose to nearly 4000.

Many small mites, Collembola, and some ants undoubtedly are lost during hand sorting.

FAUNA OF THE LOW-GROWING VEGETATION

The sweepings of the vegetation were mainly taken from the ferns of the forest floor and the ubiquitous thatch palms. It is entirely possible that many of the invertebrates were high up in the forest canopy and hence were entirely missed.

Here again, we can compare these results with the work of Shelford. During a comparable period, Shelford (in a personal communication) reports at least 10 times as many animals per square meter in the deciduous forest as we found in the tropical rain forest. Our average was approximately 32 individuals per square meter (Table III).

TABLE III. Analysis of fauna obtained from 48 sweeps of herb layer. This represents the fauna over one square meter of surface

Date: (July)	7	9	12	14	16	18
Planarian	.....	.....	1	.....	.....	.....
Earthworm	.....	.....	1	.....	.....	.....
Gastropod (snail)	.....	1	.....	.....	.....	1
Acarina (mites)	12	11	7	2	1	.....
Ticks	.....	.....	.....	2	.....	.....
Opiliones	.....	.....	3	.....	.....	.....
Araneae (spiders)	7	9	6	6	1	2
Diplopoda	.....	.....	.....	.....	1	.....
Collembola	.....	.....	1	1	.....	.....
Orthoptera	1	.....	.....	.....	.....	.....
Gryllidae	.....	.....	.....	.....	.....	1
Blattidae	.....	.....	.....	1	.....	.....
Phasmidae	.....	.....	.....	.....	1	.....
Locustidae	.....	.....	.....	.....	.....	1
Tettigoniidae	.....	.....	1	1	.....	.....
Dermaptera (earwigs)	.....	.....	.....	.....	.....	1
Corrodentia (Psocidae)	1	1	.....	.....	.....	.....
Thysanoptera	.....	1	.....	.....	.....	.....
Hemiptera	4	.....	2	.....	.....	.....
Anthocoridae	.....	1	.....	.....	.....	.....
Miridae	.....	.....	.....	2	.....	.....
Reduviidae	.....	.....	.....	.....	1	.....
Cercopidae	1	.....	.....	.....	.....	.....
Cicadellidae	3	.....	4	1	3	.....
Membracidae	.....	1	.....	.....	.....	.....
Trichoptera (caddis flies)	.....	.....	.....	.....	1	.....
Lepidoptera						
Heterocera	.....	2	.....	1	.....	.....
Rhopalocera	.....	1	.....	.....	.....	.....
Coleoptera						
Cerambycidae	.....	1	.....	.....	.....	.....
Erotylidae	.....	1	.....	.....	.....	1
Coccinellidae	.....	1	.....	1	.....	.....
Anobiidae	.....	.....	.....	1	.....	.....
Cryptophagidae	.....	.....	.....	.....	1	.....
Dascillidae	.....	1	.....	.....	.....	.....
Carabidae	.....	.....	.....	.....	1	.....
Leiodidae	.....	.....	.....	.....	.....	1
Curculionidae	.....	3	2	2	.....	.....
Hymenoptera	.....	.....	7	1	1	.....
Formicoidea	Numerous	11	16	6	3	3
Diptera	2	2	3	1	.....	.....
Insect larvae	1	.....	1	1	.....	.....
Salamander	.....	.....	1	.....	.....	.....
TOTAL	32+	48	56	30	15	11

ANALYSIS OF ANIMALS COLLECTED

Earthworms. The earthworms were relatively abundant in the soil; thus must play an important role in the ecology of the soil. Those found were all small and could not be identified due to their immaturity.

Gastropoda. Snails, as was to be expected in an area with such a limy soil, were quite abundant and varied. Among the species found were the following:

In the soil, *Oleacina* (*Salasiella*) *guatemalensis* (Pilsbry), *Lamellaxis* (s.s.) *guatemalensis* (Crosse and Fischer), *Synopeas beckianum* (Pfeiffer); in sweeping, *Helicina* (*Succincta*) *oweniana* Pfeiffer, *Helicina* (*Tristramia*) *zephyrina minima* Strebel; general cruising, *Helicina* (*Oxyrhombus*) *ghiesbreghti* Pfeiffer, *Helicina* (*Succincta*) *oweniana* Pfeiffer.

Onychophora. A single onychophoran was collected in the soil sample studied on July 12. They were so scarce as to appear to be of little ecological significance. This specimen represented only the third onychophoran to be found in Mexico.

Crustacea. The most conspicuous of the invertebrates encountered during the daytime was the crab *Pseudothelphusa* sp. These were found both in the streams and on the moist forest floor. Often they sprang the traps which were set for the mice. Unfortunately we were unable to obtain identifications of the sowbugs which were fairly abundant on the forest floor.

Acarina. As is usually the case in any work of this sort, the mites were abundant both in the soil and in the sweepings of the vegetation. We are certain that many were overlooked. So little is known about tropical mites that it is impossible to assess their importance.

In Berlese samples, (Haplozetidae) *Haplozetes* sp., (Belbidae) *Belba* sp., (Eupodidae) *Linopodes* sp., (Galumnidae) *Galumna* sp., (Anystidae) *Anystis* sp., (Oribatellidae) *Oribatella* sp., (Erythraeidae) *Erythraeus* sp., (Cunaxidae) *Cunaxa* near *simplex* Ewing, (Carabodidae) *Carabodes* sp.; in sweeping, (Anystidae) *Anystis* sp., (Haplozetidae) *Haplozetes* sp., (Galumnidae) *Galumna* sp., (Heterozerconidae) *Heterozercon* sp., (Acaridae) hypopi (nymphs); in the soil, (Trombidiidae) *Microtrombidium* sp., (Belbidae) *Belba* sp., (Macrochelidae) *Macrocheles* sp., (Erythraeidae) *Erythreus* sp.

Spiders. Spiders were very abundant and varied. They were found in soil samples, sweepings of the vegetation, in the Berlese samples, and when cruising. A partial listing of species found is as follows:

In Berlese samples, (Linyphiidae) *Meioneta,* n. sp., (Theridiidae) *Euryopis* sp. near *scriptipes* Banks, *Euryopis* sp. near *deridens* Gertsch; in sweepings, (Theraphosidae) *Aphonopelma* sp., (Uloboridae) *Miagrammopes* sp., (Scytodidae) *Scytodes championi* Cambridge, (Linyphiidae) *Grammonata* sp., (Argiopidae) *Nephila clavipes* Fabricius, *Pseudometa alboguttata* Cambridge, *Leucauge* sp., (Theridiidae) *Mysmena* sp., *Theridion* sp., *Janulus* sp., (Lycosidae) *Lycosa* sp., (Ctenidae) *Cupiennius* sp., (Clubionidae) *Castianeira* sp., (Thomisidae) *Tmarus* sp., (Salticidae) *Zygoballus* sp., *Amycus benignus* Peckham; in the soil, (Theraphosidae) *Aphonopelma* sp., (Pholcidae) *Pholcophorina* sp., *Modisimus* sp., (Oonopidae) *Oonopinus* sp., *Dysderina* sp., *Telchius* sp., (Symphytognathidae) *Anapisona* sp., (Linyphiidae) *Meioneta* sp., (Theridiidae) *Euryopis* sp., *Mysmena* sp., *Dipoena* sp., (Zodariidae) *Storena* sp., (Clubionidae) *Phrurotimpus* sp., (Salticidae) *Corythalia* sp.; cruising, (Argiopidae) *Verrucosa arenata* Walckenaer, *Eustala fuscovittata Keyserling,* (Lycosidae) *Lycosa* sp., (Ctenidae) *Cupiennius* sp., *Ctenus incolans* Cambridge, (Clubionidae) *Aysha* sp., (Salticidae) *Corythalia* sp.

Opilionids. The opilionids represented a fairly abundant group of the invertebrates. During the dry period of 1949 their number was somewhat reduced; however during the rainier period when we visited this area in 1948, they were very abundant. They were found chiefly by cruising. While they were present over the forest floor, they were more abundant under logs, among leaves, and in termite nests. A list of species found at Palenque is as follows:

(Phalangodidae) *Cynortina acanthotibialis* Goodnight and Goodnight, *Stygnomma spinipalpis* Goodnight and Goodnight, (Cosmetidae) *Cynorta apicalis* (Cambridge), *Cynorta clavipes* (Cambridge). *Cynorta clavotibialis* (Cambridge), *Cynorta serratipes* (Cambridge), *Paecilaema albonotatum* Goodnight and Goodnight, *Vonones incrassatus* (Cambridge), (Phalangiidae) *Geaya lineata* Goodnight and Goodnight, *Prionostemma foveolatum* (Cambridge).

Pseudoscorpionida. Members of the genus *Pachychitra* were encountered in many of the soil samples. They appeared to be quite abundant, for as many as three and four specimens were encountered in a single sample.

Other arachnids. Schizomids were surprisingly abundant in the soil samples. We had considered these to be very rare forms, but now feel that their absence in collections is due more to their being overlooked rather than to their lack of abundance. The tailless whip scorpions of the genus *Tarantula* were found only once in a soil sample, but were frequently encountered during cruising.

Diplopoda. In the sorting of the soil samples, nearly all of the millipedes found were immature and thus could not be identified. The mature forms were found while cruising under logs or rocks. All those which could be identified were members of the order Polydesmida, suborder Polydesmoidea:

Chondrodesmus sp., *Rhysodesmus tabascensis* Pocock, *Amplinus flavicornis* Pocock, *Atylophor* sp.

Chilopoda. Like the millipedes, these forms were best collected by cruising under logs or in vegetation. Three species were able to be identified as follows:

(Scolopendromorpha) *Newportia stolli* Pocock, (Geophilomorpha) *Pycnona vera* Chamberlin, (Lithobiomorpha) *Mayobius* sp.

Isoptera. Two species of termites, *Nasutitermes ephrates* (Holmgren) and *N. corniger* Motschulsky, were encountered numerous times. The specimens of *N. ephrates* were collected from a large nest on a tree; *N. corniger* is common in Central America, but this represents a first record from Mexico.

Corrodentia. One species, *Archipsocus nomas* Gurney (Psocidae) was captured in sweepings of the vegetation.

Odonata. The members of this order were taken only during cruising. The dragonflies were conspicuous as they flew and darted about high in the air; also they were difficult to capture.

(Zygoptera) *Cora marina* Selys., *Alamnema desiderata* Selys., *Argia cuprea* Hagen, *Argia difficilis* Selys.

Hemiptera. The Hemiptera were collected chiefly by cruising and by night collecting with a Coleman lantern. Some representative species were as follows:

(Pentatomidae) *Loxa flavicollis* Drury, *Banasa subrufescens* Westwood, *Syllobus emarginatus* Stal., *Euschistus spurculus* Stal., *Amnestus pusio* Stal., (Pyrrhocoridae) *Dysdercus mimus* (Say), (Lygaeidae) *Myodocha unispinosa* Stal., *Myodocha intermedia* Distant, *Pachybrachius bilobatus* (Say), *Ozophora concava* (Distant), (Coreidae) *Hyalmenus tarsatus* (F.), (Cryptostemmatidae) *Schizoptera hirta* McA. and M., (Reduviidae) *Zelus nugax* Stal., (Cicadellidae) [the leafhoppers were collected in sweepings of the vegetation] *Empoasca* sp., *Nesosteles* sp., *Xestocephalus* sp., *Diedrocephala sanguinolenta* (Coq.), *Agalliopsis* sp., *Homalodisca atra* (Walk.), *Draeculacephala clypeata* Osb., (Issidae) *Colpoptera* sp.

Lepidoptera. Among the most characteristic butterflies of the rain forest were the handsome, colorful Morphos. In general they were extremely difficult to capture due to their flying high in their characteristic, loping flight. They were commonly seen high above the forest paths. Other species of butterflies captured at Palenque are as follows:

Papilio sesostris zestos Gray, *Ascia monuste monuste* (Linnaeus), *Phoebis* (*Aphrissa*) *boisduvali* (Felder), *Mechanitis lycidice californica* Reakirt, *Dione juno huascama* Reakirt, *Caligo oileus scamander* Boisduval, *Pyrrhogyra edocla arenaria* Fruhstorfer, *Anartia jatrophae luteipicta* Fruhstorfer, *Anartia fatima venusta* Fruhstorfer, *Dynamine dyonis* Geyer, *Smyrna blomfildia datis* Fruhstorfer.

Coleoptera. The beetles, of course, were the most abundant of the insects encountered. They were in the soil samples, in the sweepings of the vegetation, in cruising, and many came to light at night. The most amazing of the beetles were the members of the genus *Pyrophorus* (Elateridae). These large beetles fly close to the ground, occasionally illuminating the area below them. Stevens (1841) described these remarkable beetles at great length; they have long been associated with these ruins.

(Cerambycidae) [except for *Moneilema* which was collected in a soil sample, all the cerambycids were collected from low-growing vegetation]. *Mallodon angustatum* Thoms., *Hammaticherus castaneus* Bts., *Elaphidion coronatum* White, *Nyssodrys* sp., *Moneilema* sp., (Carabidae) *Onota angulicollis* Bates [night collecting], *Lebia* sp. [from sweepings], (Elateridae) [all were collected at night], *Calais* sp., *Chalcolepidius* sp., *Pyrophorus* sp., *Monocrepidius* sp., (Scarabaeidae) [most of these were collected by cruising. The capture of *Phyllophaga cinnamonea* Blanchard represents an unusual find, for there are only three other records for this species]. *Onthophagus* sp., *Ataenius criborthorax* Bts., *Diplotaxis* sp., *Canthon femoratus* Chev., *Pelidirata punctulata* Bts., *Cyclocephala cuernavicana* Csy., *Cyclocephala sanqiunicallis* Burm., *Sycomedes mniszechi* Thoms., (Staphylinidae) [all species but *Belonuchus* were collected either from the leaf mold or soil. *Belonuchus* was swept from low growing vegetation] *Thoracophorus brevicristatus* Horn, *Stilicopsis* sp., *Coproporus inflatus* Horn, *Pseudolispinodes* sp., *Osorius* sp., *Platystethus* sp., *Belonuchus* sp., (Bostrichidae) [the single species collected, *Tetrapriocera longicornis* (Olivier) was encountered during cruising. This form occurs throughout the neotropical region.]

Hymenoptera. The only members of this order which we were able to have identified were the ants. Most of those collected were members of the subfamily Myrmicinae, *Wasmannia auropunctata* (Roger). According to a personal communication from W. M. L. Brown, Jr., it has been found to form an equally great preponderance in Berlese samples taken in several other localities of Tabasco and Veracruz. He believes it may be the commonest ant of this region. Army ants, *Eciton* sp., and the fungus or parasol ants of the tribe Attini were abundant throughout the forest. Species of ants which we were able to have identified are as follows: (Pomerinae) *Belonopelta deletrix* Mann, *Prionopelta* sp., *Ponera nitidula* Emery, *Neoponera unidentata* Mayr, *Pachycondyla harpax* (Fabr.), (Myrmicinae) *Wasmannia auropunctata* (Roger), *Lachnomyrmex scrobiculatus* Wheeler, *Macromischa azteca* Wheeler, *Solenopsis* (*Diplorhoptrum*) sp., *Pheidole* sp., *Rogeria* sp., *Octostruma* sp., *Smithistuima* (*S.*) *margaritae* (Forel), *Tachnomyrmex scrobiculatus* Wheeler, *Strumigenys* (*Str.*) *ludia* Mann, (Pseudomyrminae) *Pseudomyrma* sp., (Dolichoderinae) *Monacis bispinosus* (Olivier), (Formicinae) *Brachymyrmex* sp., *Paratrechina* sp., *Camponotus* sp.

Amphibia. Only two salamanders were found, one surprisingly enough showing up in a sweeping of vegetation! The two species were *Bolitoglossa moreleti* Smith and *Bolitoglossa rufescens* (Cope).

Among the frogs and toads, the most interesting specimen encountered was *Eleutherodactylus laticeps* (Duméril). Originally it was collected in 1847 or 1848, but the exact locality was not certain. Other frogs collected by cruising through the forest and along the streams were as follows:

Eleutherodactylus rugulosus (Cope), *Eleutherodactylus rhodopis* (Cope), *Eleutherodactylus conspicuus* Taylor and Smith, *Centrolenella fleischmanni* (Boettger), *Bufo valliceps macrocristatus* H. M. Smith.

Reptilia. Lizards were abundant throughout the forest, but were most conspicuous in the clearings and about the ruins. The small brown snake, *Rhadinaea decorata* (Günther), was extremely abundant upon the forest floor, but also very difficult to capture as it crawled rapidly away among the vegetation. One specimen of *Imantodes cenchoa leucomelas* Cope was captured, and a few coral snakes were seen. The fer-de-lance and boa constrictor are both known to be abundant throughout this area although we did not encounter any. Among the lizards captured were these:

Anolis lemurinus bourgeaei Bocourt, *Anolis humilis uniformis* Cope, *Sceloporus teapensis* Günther, *Basiliscus vittatus* Wiegmann, *Scincella cherriei cherriei* (Cope), *Eumeces sumichrasti* (Cope), *Ameiva festiva edwardsii* Bocourt.

Aves. Many observations were made of the birds in as many areas as was possible. These included the forest itself, forest edges, clearings, and stream banks. Dr. R. E. Tashian devoted his time to making a collection of birds and to making observations on their habits whenever possible. He has reported his findings in a detailed paper (Tashian 1952). In this paper we are listing only the commonest birds in the areas where they were seen most frequently. It is clear that no bird is confined to any one habitat; thus many of the birds that were common in the low trees also were seen from time to time in the high trees. The forest edge was an artificial boundary caused by clearing devoted to agriculture; thus the birds found here were also found in the undergrowth of the forest. The seed-eating birds such as the parrots, *Pionus senilis senilis* (Spix), and the icterids were constantly raiding the cornfields to the despair of the local inhabitants.

Of particular note were the many mixed flocks consisting of many different species of small birds. These flocks were particularly abundant along the clearings though many were observed within the forest itself. This latter type of flocking was most noticeable when an ant colony was on the march. The most conspicuous flocks were those of the parrots whose bright colors and noisy chatterings attracted attention in the morning and evening as they went and came from their feeding grounds.

In the following listing, an attempt is made to distinguish the various birds by the habitats in which they were most frequently seen.

High forest: *Sarcoramphus papa* (Linnaeus), king vulture; *Coragyps atratus* (Bechstein), black vulture; *Buteo magnirostris griseocauda* Ridgway, Mirador insect hawk; *Leucopternis albicollis* (Latham), white hawk; *Pionus senilis senilis* (Spix), white-crowned parrot; *Ciccaba nigrolineata* Sclater, black and white wood owl; *Campylopterus hemileucurus hemileucurus* (Lichtenstein), De Lattre's sabre-wing; *Trogon massena massena* Gould, Massena trogon; *Momotus momota goldmani* Nelson, Goldman's motmot; *Ramphastos sulfuratus* Lesson, keel-billed Toucan [usually seen in flocks of eight to ten individuals]; *Pteroglossus torquatus torquatus* (Gmelin), collared aracari; *Phloeoceastes guatemalensis guatemalensis* (Hartlaub), Guatemalan ivory-billed woodpecker; *Microrhopias quixensis boucardi* (Sclater), Boucard's ant-wren; *Cyanerpes cyaneus carneipes* (Sclater), Central American blue honey creeper; *Caryothraustes poliogaster poliogaster* (Du Bus), bishop grosbeak [noted in flocks of 15 to 18].

Ground and low vegetation: *Tinamus major* (Gmelin), greater tinamou; *Crax rubra rubra* Linnaeus, great curassow; *Malacoptila panamensis inornata* (Du Bus), white-whiskered soft-wing; *Xiphorhynchus flavigaster eburneirostris* Des Murs, ivory-billed woodhewer [associated with mixed flocks]; *Dendrocolaptes certhia sancti thomae* Lafresnaye, barred woodhewer; *Formicarius analis moniliger* Sclater, Mexican ant thrush; *Attila spadiceus flammulatus* Lafresnaye, flammulated attila [observed in mixed flocks]; *Lipaugus unirufus unirufus* Sclater, rufous piha; *Pachyramphus cinnamoneus fulvidior* Griscom, cinnamon becard; *Pipra mentalis mentalis* Sclater, yellow-thighed manakin; *Myiobius sulphureipygius sulphureipygius* (Sclater), sulphur-rumped myiobius [observed in small mixed flocks]; *Onychorhynchus mexicanus mexicanus* (Sclater), Mexican royal flycatcher; *Platyrinchus mystaceus cancrominus* Sclater and Salvin, Mexican spade billed flycatcher; *Elaenia viridicata placens* Sclater, placid elaenia [observed in flocks of 10 to 14 birds]; *Campylorhynchus zonatus restrictus* Nelson, Tabasco cactus wren or banded wren; *Thryothorus rutilus umbrinus* Ridgway, Guatemalan spotted-breasted wren; *Henicorhina leucosticta prostheleuca* (Sclater) Sclater's wood wren [often found associated with *Thryothorus rutilus*]; *Tanagra gouldi gouldi* (Sclater), Gould's euphonia [a common flocking species]; *Phlogothraupis sanguinolenta sanguinolenta* (Lesson), crimson-collared tanager; *Habia rubica rubicoides* (Lafresnaye), Mexican ant tanager [observed in flocks, associated with other tanagers]; *Lanio aurantius aurantius* Lafresnaye, Mexican shrike tanager [found in small flocks]; *Cyanocompsa cyanoides concreta* (Du Bus), blue-black grosbeak; *Seiurus motacilla* (Vieillot), Louisiana water-thrush.

Forest edge: *Buteo magnirostris griseocauda* Ridgway, Mirador insect hawk; *Columba nigrirostris* Sclater, short-billed Pigeon; *Columbigallina talpacoti rufipennis* (Bonaparte), ruddy ground dove; *Claravis pretiosa* (Ferrari-Perez), blue ground dove [often seen in flocks]; *Pionus senilis senilis* (Spix), white-crowned parrot [usually observed in flocks]; *Melanerpes pucherani perileucus* (Todd), white-barred woodpecker; *Pachyramphus cinnamomeus fulvidior* Griscom, cinnamon becard;

Megarhynchus pitangua mexicanus (Lafresnaye), Mexican boat-billed flycatcher [seen in small flocks]; *Myioztetes similis texensis* (Giraud), vermilion-crowned flycatcher or social flycatcher; *Pitangus sulphuratus guatimalensis* (Lafresnaye), Central American derby flycatcher; *Elaenia viridicata placens* Sclater, placid elaenia [noted in flocks]; *Leptopogon amaurocephalus pileatus* Cabanis, brown-capped leptopogon [seen in small flocks]; *Campylorhynchus zonatus restrictus* Nelson, Tabasco cactus wren [found in flocks of 8 to 12]; *Amblycercus holosericeus holosericeus* (Lichtenstein), Prevost's cacique; *Icterus prosthemelas prosthemelas* (Strickland), Strickland's oriole; *Icterus mesomelas mesomelas* (Wagler), yellow-tailed oriole; *Tanagra lauta lauta* Bangs and Penard, Bonaparte's euphonia [secured from flocks in marginal forest]; *Tanagra nigrocincta larvata* (Du Bus), golden-masked tanager [collected from a mixed flock]; *Ramphocelus passerinii passerinii* Bonaparte, Passerini's tanager; *Habia rubica rubicoides* (Lafresnaye), Mexican ant tanager [a common flocking species]; *Sporophila torqueola* Bonaparte, cinnamon-rumped seedeater; *Volatinia jacarina splendens* (Vieillot), Northern blue-black grassquit [found in flocks]; *Arremonops conirostris chloronotus* (Salvin), greenbacked sparrow.

Mammalia. Mammals were trapped, hunted, and observed whenever possible. Observations were difficult due to the dense forest cover and the secretive habits of most of the forms. The only conspicuous forms were the spider and howler monkeys. The spider monkeys often roamed around the ruins and through the forests in groups of 15 to 20 individuals; the howlers were frequently heard roaring in the early morning and evening.

Quantitative trappings of selected plots in the forest gave an estimated abundance as follows: white-footed mouse, 20 per hectare, and lesser climbing rat, 8 per hectare. It was impossible to obtain quantitative estimates of the other mammals. In fact, many of the mammals whose presence was reported by local residents or evidence of which were easily observed were not collected. Among these were such an abundant form as the collared peccary which trampled down the vegetation and from time to time were frightened up along forest trails, the white-lipped peccary, many different cats, the small forest deer, and the armadillo. These are all discussed by Del Toro (1952). A list of the mammals collected during our stay is given here; further details can be found in Kuns and Tashian (1954).

Caluromys derbianus aztecus (Thomas), white-eared woolly opossum; *Philander opossum pallidus* (Allen), four-eyed opossum; *Didelphis marsupialis* Linnaeus, black-eared opossum; *Saccopteryx bilineata* (Temminck), white-lined bat; *Peropteryx macrotis macrotis* (Wagner), sac-winged bat; *Pteronotus davyi fulvus* (Thomas), naked-backed bat; *Carollia perspicillata azteca* Saussure, short-tailed bat; *Artibeus lituratus palmarum* Allen and Chapman, Trinidad fruit bat; *Artibeus jamaicensis yucatanicus* (Allen), Jamaica fruit bat; *Desmodus rotundus murinus* Wagner, vampire bat; *Myotis nigricans extremus* Miller and Allen, little black bat; *Alouatta palliata mexicana* Merriam, black howler monkey; *Ateles geoffroyi vellerosus* (Gray), Mexican spider monkey; *Sciurus aureogaster hypopyrrhus* (Wagler), fire-bellied squirrel; *Sciurus deppei deppei* Peters, Deppe's squirrel; *Heteromys desmerestianus desmerestianus* Gray, spiny pocket mouse; *Tylomys nudicaudus nudicaudus* (Peters), climbing rat; *Ototylomys phyllotis guatemalae* Thomas, lesser climbing rat; *Peromyscus mexicanus teapensis* Osgood, Mexican white-footed mouse; *Cuniculus paca nelsoni* (Goldman), paca; *Nasua narica narica* (Linnaeus), coati; *Potos flavus campechensis* Nelson and Goldman, kinkajou; *Eira barbara senex* (Thomas), tayra; *Tagassu tajacu* subspecies, collared peccary.

STREAM STUDY

Just behind the main area of the ruins was a small stream which was bordered with heavy vegetation. The stream itself consisted of a series of small pools whose sides were built up by the lime precipitated from the water of the stream. The pools varied in size from many less than a meter across and very shallow to a few large pools up to seven meters across and one or more meters in depth. So heavy was the load of calcium carbonate in the stream that the shells of dead snails were quickly encrusted. The water was very basic in its reaction.

When the air temperature was 28°C, the water temperature was 25°C. During the period of our study, the depth of the stream varied from a few inches in the rapids to a depth of one or more meters in a few of the larger pools. The bottoms of the small pools were thickly covered with small pebbles and the lime-encrusted shells of dead snails.

A few quantitative observations of the inhabitants of the stream were made. Under the rocks in an area approximating 600 square centimeters, we found three stonefly nymphs, one mayfly naiad, and three snails. An area approximately 0.1 meter square in the rapids where the water was less than one-half meter in depth had a school of 12 to 15 fish (*Priapella compressa* Alvarez), one small fresh water shrimp (*Macrobrachium* sp.), and one snail. In the same area, under a large rock, there was one damsel fly nymph and one mayfly naiad. Under some small rocks we found one stone fly naiad and another mayfly naiad, and another species of snail.

In a pool with a pebbly bottom and very shallow water, there were no fish, nine individuals of one species of snail, and another individual of a larger species of snail.

In a seine haul covering approximately seven by three meters, 44 fish (*P. compressa*) and 19 small shrimp (*Macrobrachium*) were collected.

In addition to the species collected above, cruising yielded the unusual fish *Symbranchus marmoratus* Bloch, freshwater crabs (*Pseudothelphusa* sp.), the large shrimp (*Macrobrachium jamaicense* (Herbst), water striders, several groups of gyrinids (*Gyretes acutangulus* Sharp), and a dytiscid (*Laccophilus* sp.). Two species of snail were found, but we unfortunately have not been able to have them identified.

SUMMARY

Though there has been an increasing interest in the fauna and flora of the rain forests of the neotropical region, only a few studies have been made in which an analysis of the total fauna has been attempted. This present study was undertaken during the summer of 1949 in the undisturbed rain forest surroundng the archeological site near Palenque, Chiapas, Mexico. Though we were handicapped by the difficulty of getting material identified and by the fact that methods for the study of such forests have not been sufficiently devised, we feel that a study such as this does contribute to our understanding of tropical ecology.

The study area was located five miles southwest of the town of Palenque, Chiapas, Mexico, in the foothills of the Sierra de Palenque at an altitude of about 210 meters. The town has an annual rainfall of 3200 mm. Surrounding the archeological ruins was an undisturbed, canopied rain forest with many layers of vegetation. The herbaceous layer covered about 60% of the ground, the shrub layer approximately 40% to 50%, the low tree layer 100%, and the high tree layer, also 100%. Many epiphytes, bromeliads, and vines were in the canopy trees.

The methods of study were essentially those outlined by Shelford (1951) as based on his work in the temperate zone. The leaf litter and soil were sampled by gathering 0.1 square meter and carefully sorting; the herb and shrub layers were sampled by means of a beating net. Forty-eight sweeps was considered to represent the fauna over a square meter of soil. These samples were supplemented by use of field Berlese funnels and intensive cruising under logs, in leaf litter, in termite nests, under rocks, and in other possible locations. Reptiles and amphibians were collected whenever and wherever possible; birds were studied by cruising and could only be indicated as to relative abundance. Mammals were trapped and hunted. Some quantitative trapping of quadrats was undertaken.

Observations were also made of various climatic factors, including temperature, humidity, and light available. As this study was made toward the end of the dry season, just before the start of the rainy season, there were not the typical daily rains. The temperature in the clearing near the ruins varied from a low of 22.8°C taken at 8:00 A.M. the morning of July 17 after a heavy rain to a high of 32°C at 4 P.M. on the afternoon of July 19. The lowest humidity was 58% on July 9 at noon, while the highest recorded was during and directly after rainstorms. Comparable data taken in the forest showed that in general the temperature was slightly lower and the humidity slightly higher. Due to the heavy forest cover, the light available to plants varied from 0.2 foot-candles in a shaded dry arroyo to 3.2 foot-candles in a small clearing within the forest. In an area denuded of vegetation by ants, 200 foot-candles were recorded.

The soil fauna averaged 407 individuals per square meter and the fauna of the low-growing vegetation averaged 32 individuals per square meter. Quantitative trapping gave an estimated population of 20 per hectare of the white-footed mouse (*Peromyscus mexicanus teapensis* Osgood) and 8 per hectare of the lesser climbing rat (*Ototylomys phyllotis guatemalae* Thomas). It was impossible to estimate the bird population due to the difficulty of observing the birds in the forest.

In the soil, the earthworms appeared to be relatively abundant, thus must play an important role in the ecology of the soil. Snails, mites, spiders, immature millipedes, centipedes, many different beetles, and numerous larvae were all found in the soil. In the sweepings of the vegetation, many mites, a few snails, spiders, opilionids, hemipterans (including many leaf hoppers), numerous beetles, and hymenoptera were found. Ants were encountered in both soil and sweeping samples. General cruising of the area proved to be the most effective method for collecting adult species of insects. Many large beetles, spiders opilionids, damselflies, hemipterans, butterflies, ants, and termites were thus collected. Night collecting with a lantern supplemented the general day cruising.

Among the vertebrates, numerous frogs, lizards, snakes, a few salamanders, many birds, and mammals were observed. Cruising through the forest was the most effective method of observing all these forms.

A brief survey of a small stream revealed that there was quite a diversity of forms includng many insect nymphs, numerous fish, two species of fresh water shrimp, water striders, gyrinids, and many snails.

The great diversity and abundance of this fauna impresses one with the great need for further studies of the coactions and reactions of the various animals. A study such as this indicates some of the problems involved. Much still remains to be learned of proper methods of census and study of the many complex interrelationships that prevail in such a forest.

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FUNGUS-GROWING ANTS AND THEIR FUNGI: *TRACHYMYRMEX SEPTENTRIONALIS*

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The present studies were undertaken primarily as an investigation into the factors responsible for the production of thriving cultures of fungi in the ant gardens despite the continual bringing in of contaminants (Weber 1954, 1955). When the ants are removed from their gardens the ant fungus is quickly replaced by alien fungi and bacteria, and it is only in the symbiotic association between the ants and their fungus that a healthy garden is maintained which permits both organisms to survive. Neither is found in nature without the other. The association is one of considerable complexity and the behavior and general biology are among the relevant factors.

The northernmost of all fungus-growing ants is *Trachymyrmex septentrionalis* McCook, which is an ant of the eastern United States extending as far north as Long Island, New York. The general summer habits of the ants have been made known through a succession of students beginning with McCook (1880), Morris (1881) and Wheeler (1907). Attention in the present report has been concentrated on the habits of the ants as they bear on the maintenance of the garden.

ADAPTATIONS TO THE NORTHERN CLIMATE

Trachymyrmex septentrionalis is active in New Jersey for a short time in the year compared with the year-long activity of tropical *Trachymyrmex*. In a normal year April is probably the earliest month for the resumption of activity. March in New Jersey may have suitable periods of air temperatures but the sandy ground, in which the ants nest, lags in warming.

March 19, 1955 temperatures at the site of all nests specified below, the intersection of U. S. Highway 322 with the boundary between Atlantic and Gloucester Counties, except the first one of September 26, 1953, illustrate a condition unfavorable for ant activity. The temperatures were (at 11:45 a.m.-12:05 p.m.) as follows:

Surface of white sand in sun	14.8°C
Surface of white sand in shade	11.5°C
Depth in sand of 10 cm	6.0°C
Depth in sand of 20 cm	5.5°C
Depth in sand of 25 cm	5.2°C
At height of 100 cm in sun	13.2-13.8°C
At height of 100 cm in shade	12.0-12.6°C

At a second and nearby site at 12:20 pm the sand surface in the sun was 15.5° at a depth of 10 cm it was 8° and at 50 cm it was 5.5° C.

No ants of any kind were active here and no craters of any species were in evidence. Several spiders were the only arthropods represented and flecks of snow remained on nearby shaded north slopes from a wet snowfall of the preceding day.

April 9, 1955, again at the usual site, temperatures (at 11: 23-30 am) were still too low for *Trachymyrmex* activity and were as follows:

Surface of white sand in sun	33.5°C
Depth in sand of 10 cm	14.5°C
Depth in sand of 25 cm	9.5°C
Depth in sand of 40 cm	9.2°C
At height of 100 cm in sun	21.7-23.1°C
At height of 100 cm in shade	20.2-20.6°C

Although the weather was cold for this ant, other ants were resuming activity here (*Leptothorax* sp. and *Tapinoma sessile* Say). About 10 miles away in the same Pine Barrens type of habitat but on a slight rise or mound where the ants had previously been found to be common, the temperatures on the same day at 3:10-3:15 pm were as follows:

Surface of white sand in sun	29.6°C
Depth in sand of 25 cm	13.2°C
Depth in sand of 50 cm	10.8°C
At height of 100 cm in sun	22.8-23.8°C
At height of 100 cm in shade	22.2°C

The difference in subsurface temperatures at the two sites on this day was probably due to the difference in insolation and drainage.

Other ants that had resumed activity included *Formica* sp. This and *Leptothorax* and *Tapinoma* are common Holarctic genera compared with the *Trachymyrmex*, which is a Neotropical derivative.

April 1955 turned out to be an unusually cold month and final records for the month (at 11-11:15 a.m. EDST) on the 30th at the usual site were as follows:

Surface of white sand in sun	28.1-28.5°C
Depth in sand of 10 cm	15.4°C
Depth in sand of 20 cm	12.4°C
Depth in sand of 30 cm	12.3°C
Depth in sand of 40 cm	12.3°C
Depth in sand of 50 cm	11.9°C
At height of 100 cm in sun	21.2-22.4°C
At height of 100 cm in shade	20.9-21.2°C

No *Trachymyrmex* craters were found here or at numerous other Pine Barrens sites where they were known to occur. A slight knoll with full insolation on the southwest slope recorded (at 1:55 p.m.) a surface temperature of 33.2-33.5°C, at a depth of 10 cm 21.3°C and at a depth of 20 cm 16.4°C. Other ants were fully active, including *Lasius* (*Acanthomyops*) sp. and *Camponotus pennsylvanicus ferruginea* (Fabr.).

On April 25, 1954 the ants appeared to have but recently resumed activity. Unfortunately no temperatures were taken. Craters were poorly developed. Under one at a depth of about 15 cm was a chamber, empty except for dense clusters of ants. Under this was another of irregular shape containing one female, with a small gaster, and workers. Under a second crater at a depth of 5-30 mm was a chamber 2 cm in diameter containing a dense, quiescent cluster of ants. Beneath this at a total depth of 12 cm was what seemed to be an abandoned garden of golden brown color. The integument of the ants was glistening and immaculate compared with the duller appearance later in the season. There was no fluffy fungus-garden of the kind developed by the ants during the summer. The over-wintering remnants were in the form of small masses of dark pellets of substrate with no obvious fungal growth. By the following day, under laboratory temperatures of about 23°C., hyphae of the fungus had developed as are normally present in the summer. May 15, too, was early in the year for full activity and nests in the field contained small fungus gardens on dark substrate. Later in May, 1954 the ants became fully active and this was also true on May 25, 1947. June appears to be the month with greatest activity and from then to early September they are typical attines in their behavior. The literature on this species deals with the ants in this period.

The external appearance of a typical nest is shown in Figure 1. On September 16, 1953 the ants were active and first chambers were found under three nests at depths of 15, 15 and 30 cm, respectively, only one of which contained a garden. One male had survived to this late date. On September 26 the ants were still active. Under one crater a chamber was found at a depth of 2-5 cm which was empty except for a cluster of workers and pupae. The nest was in gray sand with an admixture of small pieces of charcoal from a recent scrub fire. The presence of pupae at this shallow depth in dark sand fully exposed to the sun was probably an adaptation to the climate. The warmth at the site would enable the final stage of the brood quickly to mature before cold weather. Two other nests had chambers at a depth of 15-20 cm which had fungus gardens estimated to fill not over ¼ to $\frac{1}{10}$ of the space. This, also, may have been a response to the climate, the ants having brought up the gardens from deeper chambers in response to the resumption of warm weather. No deep chambers were found under several nests to depths of 75 cm. Similar observations were made a year later. On October 31, 1953 the ants were obviously inactive and could only be found at the site of formerly excavated nests when these could be located. At a depth of 15-20 cm a small cluster of workers was finally

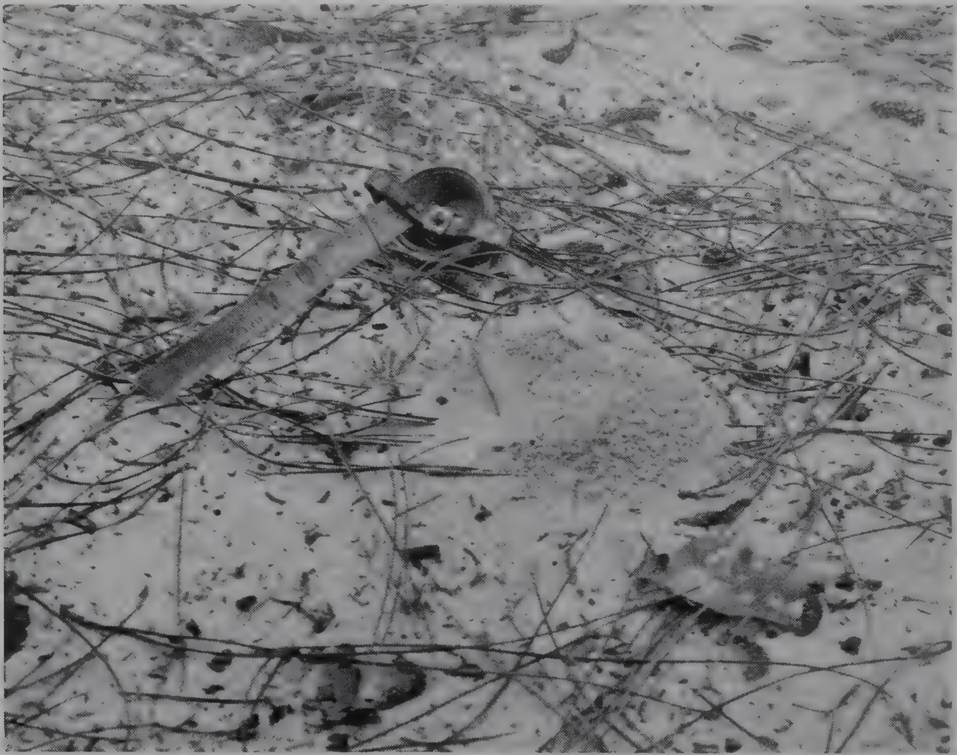

FIG. 1. Crater entrance to the nest of the form known as *Trachymyrmex septentrionalis seminole* Wheeler from southern Florida. This is also typical of the New Jersey *T. septentrionalis* and the size and shape of the crater are duplicated by colonies in the laboratory. Size indicated by tape measure ruled in centimeters. Phot. Richard Archbold.

discovered. These were sluggish though they responded quickly to warmth. Their chamber did not contain remnants of a garden. Unfortunately no September-October temperatures are available. By early December external indications of the nests have been largely erased by the weather and in one search under 30 probable sites no workers could be found at depths up to 50 cm.

The above observations suggest that the brood is matured by September and none is carried over to the next year. The fungus gardens deteriorate later in the fall but may be developed somewhat in response to warm periods in September-October. The ants then cluster together in tunnels or small chambers in the sand, probably at variable depths depending on the moisture, and hibernate until the spring. It is entirely possible that there is a high mortality rate among the workers. During April activity is resumed and gardens quickly developed. The over-wintering stage of the fungus is unknown but may be hyphae or bromatia in the form of somewhat sparse remnants on dark and aged substrate left in the chambers, and must also be in a "hibernating" condition. No indication of conidia formation or sporulation is known.

Overwintering Laboratory Colonies

New Jersey colonies were kept in the laboratory during the winters of 1953-54 and 1954-55.

They were kept in observation nests which consisted of a variety of Plexiglas and glass containers. The standard (Fig. 2) for the overwintering colonies was of Plexiglas with inside dimensions of 205 mm in length, 152 mm in width and 18 mm in depth. It was divided into three approximately equal rectangular chambers by two partitions at right angles to the sides, each chamber connected with the others by small holes in the partitions. This arrangement permitted varying conditions of humidity in the chambers and one could be used for introducing substrate without disturbing pendant gardens in the other two. The standard nests were placed in a large photographic enamel pan, rimmed with petroleum jelly to contain the ants, and this constituted the arena. The microcosms or isolated small portions of nests were in 90 x 17 mm glass Petri dishes (Fig. 3).

During the first winter, i.e. in October, the colonies were merged into one which contained three females. At this time there was a flourishing garden which gradually became smaller in November. By December 22 (at about 18°C) there were many active ants but only tiny remnants of a garden. This was deemed insufficient as a source of food and they were supplied with the monosaccharide, corn sugar syrup. They were also seen to eat peanut butter and canned dog food although these were trivial sources of food. By December 26 the garden was reduced to several isolated fragments, each about one millimeter in diameter. The ants moved sluggishly at 16°C. Subsequently it was found that at 13°C they may slowly wave their antennae when disturbed and slowly move about. Below this temperature they clustered together with legs held close to the body and became immobile. By early February each fragment had about doubled in size and February 26 there were two gardens, the smaller of which was larger than the total bulk of December. February temperatures had been 16-18°C.

Temperatures in this laboratory after early February, 1954 were recorded by means of a Taylor maximum and minimum thermometer (Taylor Instrument Co., Rochester, N. Y.) and by a continuously recording Bacharach Tempscribe instrument (Bacharach Industrial Instrument Co., Pittsburgh, Pa.). The one window of the laboratory was kept closed, except in late May and June, 1954, and temperatures fluctuated slowly. The mean of the daily maximum and minimum gives approximately the temperatures during most of the hours. From December, 1953 to October, 1954 the radiator was turned off and the general warmth of the building was the sole source of heat.

On March 2 the garden was flourishing and there was much activity. Substrate was being added faster than the garden could grow. The substrate which was always made available to the colonies was farine (granulated cassava starch). From March 2 to 24 temperatures were mostly 18-22°C with an occasional rise to 23° and during this three-week period four fragments had developed with an estimated total bulk of about three cubic centimeters. No brood was visible. The ants had now carried out sand grains through a narrow aperture in the container and created a full-size semicircular crater as they would have done in nature during April. On April 20 the first eggs were noted and the three females stationed themselves by a cluster of about a score. After April 20 temperatures were generally 22-24°C until the end of May, when they rose. On June 3 occasional rises to 29°C occurred and during this month the colony was merged with others.

During the summer of 1954 many males were produced by the merged colonies but no females. Luxuriant gardens were produced despite variable June extremes of 23-33°C. In July and August the merged colonies were kept in a dark basement room at a temperature generally 20-24°C. At the end of August they were brought back to the laboratory.

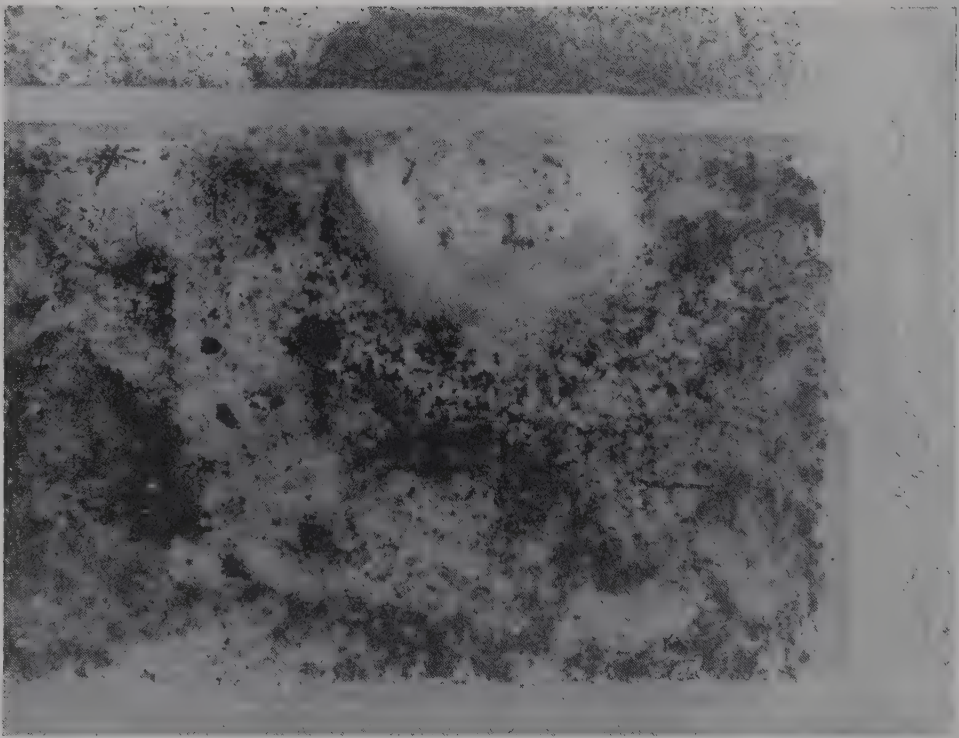

FIG. 2. Standard observation nest showing a portion of a colony of the New Jersey *Trachymyrmex septentrionalis* McCook which has developed a fungus-garden from artificially cultured fungus of the Panama *Atta colombica tonsipes* Santschi. The ants always remove soil from the immediate vicinity of the garden and in nature support it on rootlets. Substrate (farine) for the fungus has been introduced on the right. Phot. Lloyd Merritts.

During the second winter laboratory temperatures were generally 18-26°C with a common daily range of 18-25°C. The flourishing fungus garden became reduced as before and no brood was noted after September. Numbers of ants were removed for experiments from time to time but the total population remained higher than the first winter and there were at least six females, all of which were compatible and were generally in the same area of the garden. Again, the low point in garden bulk was reached in December and January. During early December the ants generally remained in what may be termed a hibernating condition, since it resembled that found in nature. The ants clustered tightly together, each with legs drawn close to the body and with the femora and tibiae folded together. They remained motionless for long periods. During January a gradual build-up of the garden took place as in the previous year. Eggs were first noted on March 10. Mites appeared in portions of nests, in sand, in the garden, or on the ants and a March 26 collection from a worker ant was identified as *Ereynetes* sp. by Dr. G. W. Wharton.

The above incomplete data show a striking reduction in activity during the winter despite moderate temperatures. A factor in initiating inactivity may be the removal of the stimulus of a developing brood. In this case the female, as part of her adaptation to a northern climate, may exhaust her egg-laying capabilities in the late summer and require the September-March months at lowered temperatures gradually to develop the eggs. The sluggishness of the ants themselves of course means that they require less food, and the gardens deteriorate from lack of substrate.

A MICROCOSM

A fragment of fungus-garden with a few ants isolated on sterile nutrient agar in a Petri dish (Fig. 3) may illustrate the ability of the ants to maintain a pure fungal culture despite adverse conditions, since contamination of the agar is inevitable. The agar used in microcosms and for

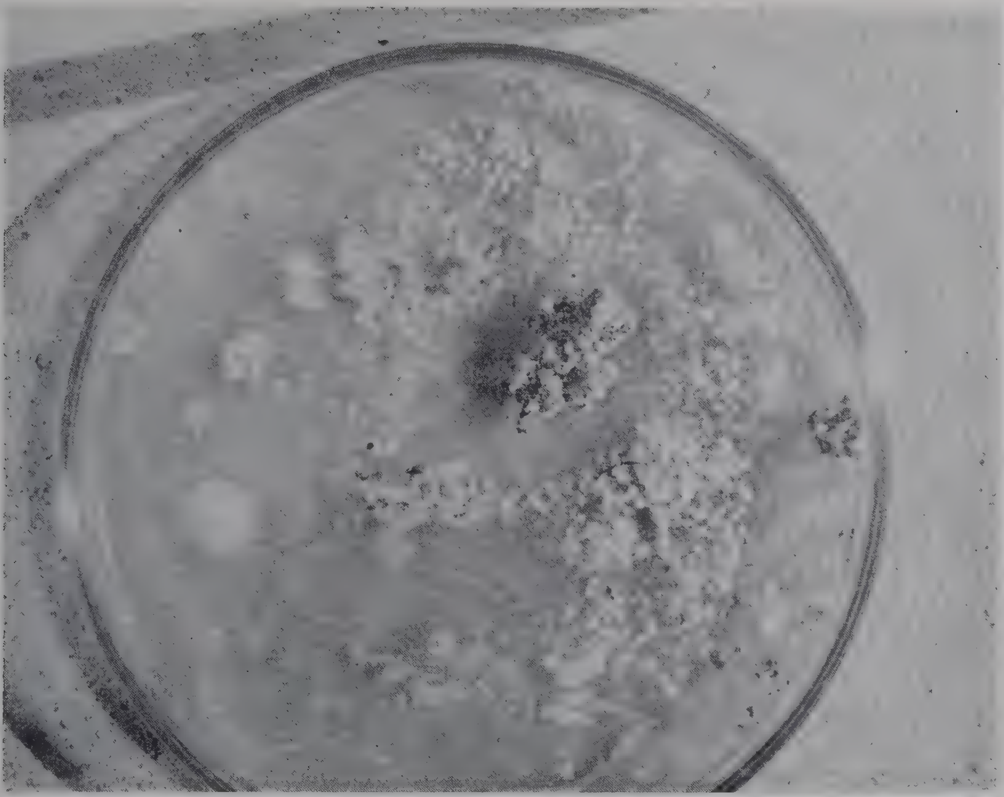

Fig. 3. Microcosm on Sabouraud's agar in Petri dish. Despite surrounding contaminants the ants maintain a small fungus-garden. Some of the agar adjacent to the garden has been cut into pieces and scattered to the side.

culturing the fungus was Sabouraud's, a Difco (Difco Laboratories, Detroit, Michigan) dextrose agar of pH 5.6, designed for cultivating molds and yeasts. The experiment was performed with many species and repeatedly with *T. septentrionalis.* Too few ants, unfavorable temperatures and too massive contamination frequently make it impossible for the garden to be maintained. A successful experience with *T. septentrionalis* is described below, however. Examination of the microcosm was made under the binocular stereoscopic microscope and the habits observed aided in an understanding of the symbiosis.

A fragment of freshly excavated garden and nine worker ants were introduced into a sterile agar Petri dish on May 15, 1954, while the author was in the field in the New Jersey Pine Barrens. By May 18 a completely normal garden was developed. The ants had cropped and re-worked the material so that it closely resembled that usually found in nature except for greater luxuriance of the fungus occasioned by high humidity. On May 19 the ants were pulling out mycelial tufts and planting them elsewhere in the garden or against the glass ceiling, using the apices of the mandibles and fore feet. One ant appeared to regurgitate to another, appressing its sub-mandibular mouthparts to the other for several seconds. On May 20 an ant remained motionless while another spent several minutes carefully licking its gaster on all sides, then went away while another came up to the first and licked various parts of the integument. By May 21 the ants had exacavated agar at the side from which daylight came and these excavated pellets remained clean. An ant spent a number of minutes lapping moisture on the glass ceiling close to the garden, which was now suspended from the ceiling. It used its hypopharynx alone, this going back and forth like a piston. The labial palpi were extended from time to time but did not appear to be used for sensory purposes as much as the tips of the antennae. A second ant spent several minutes feeding on hyphae. A tuft of mycelium would be pulled away from the substrate, then the teeth on the lacinia worked back and forth on it, the mandibles generally being kept closed. Another ant similarly ate into mycelium in several places and others were engaged in "feeling" the garden by delicately playing the apices of the antennae over it. By May 26 the garden had appeared to grow from its original estimated one-half cubic centimeter. In the meanwhile alien fungal colonies and possibly bacteria had developed on the general agar surface. An ant pulling on a mycelial tuft eventually ingested it completely. Temperatures since May 15 were 21-24°C.

On May 27 eggs were seen for the first time and were probably laid by a worker since no evidence of brood had been seen during repeated scrutiny under the microscope. A worker carried two eggs from one site to another in the garden. On May 29 three or four eggs were so heavily swathed in mycelium as to be difficult to discern. Temperatures had remained close to 24°C since the 26th. By June 2 the garden appeared less luxuriant under temperatures reaching 27°C, as though the fungus were being eaten faster than it was growing. An ant carried a shiny egg, free of fungus, for several minutes, then pressed it with the mandibular apices into place near the cluster of eggs covered with fungus. There now appeared to be seven or more. On June 2 (temperature 28°C) an ant appeared to have an enlarged gaster as though developing eggs. Another carried a shiny, clean egg. The mycelium was now much reduced and some substrate was exposed.

On June 3 (temperature 28°C) they were given particles of farine which had been dyed with 1% aqueous neutral red and then dried. This was the first time the Petri dish cover had been lifted since May 15. Within seconds one ant seized a particle and within three minutes two had been carried to the garden. Four minutes later an ant was licking a third piece and after three minutes of this it defecated on the particle while holding it with the fore legs, curving the apex of the gaster forward. The ant then took it to the underside of the garden where no further observations could be made. Within 20 minutes after the farine was introduced all but three particles had been handled by the ants, either on the contaminated general agar surface or on the garden. The piece once defecated on seemed to have later received another portion and still later received an ant's gastric tip momentarily but no transfer of liquid feces was seen. Forty minutes after the farine was introduced all particles had been licked repeatedly. Some were on the garden; one was against the cluster of eggs. Another defecation on a farine particle was observed later. Eggs both shiny and partially covered with mycelium were seen. No hyphae appeared on the new substrate within five hours.

The following day (temperature 29°C), however, mycelial tufts were on the dyed farine in such a form as to indicate clearly that the ants had planted them. About 14 eggs were estimated to be present. An area of agar 20-30 mm in diameter under the suspended garden was much excavated and was free from all contaminants or fungi of any kind. The garden itself was about 10 mm in maximum diameter.

On June 5 (temperature 28°C) the mycelial tufts on the dyed farine were growing. An ant carried five eggs rapidly out of sight; a dozen or more remained in view but were obscured by the mycelial growth on them. By June 9 (temperature 26-29°C in the interval) the growth of mycelium had rendered invisible the pink or red color of the dyed farine; the general agar surface had become much contaminated by bacteria or yeasts except in the circle below the suspended garden. By June 14 (temperature 26-32°C in the interval) all of the agar had been excavated below the garden, exposing the glass floor, and the edges of the cut agar remained free of the contamination, which was now general on the agar, as in Figure 4. Some of the peripheral mycelium turned brown, apparently from the high temperatures.

Second Month

One larva 1.5 mm and one 1.0 mm long were seen on June 15 and must have been kept on the underside of the garden for some days where they could not be seen; both were smooth and shiny. By June 17 the smaller larva had a scanty covering of hyphae, which was greater the following day (temperature 25-26°C). On June 20 (temperature 28°C) the garden, now about 14 x 8 x 10 mm, was definitely dryish. On June 21 more dyed farine was introduced, necessitating the second lifting of the glass cover since May 15. The ants immediately seized the particles and treated them as before, licking them assiduously before planting them in the garden with a side-to-side motion as they were thrust in. The garden was now estimated to be about one cubic centimeter in bulk, less than half that of June 3 but twice as much as on May 15. The variable and high temperatures and exhausted substrate were factors. The following day (temperature 28-30°C in the interval) all dyed particles were incorporated in the garden and some had mycelial tufts on them as though planted. From June 22 to 28 the garden flourished despite high (28-31°C) temperatures. The large larva was smooth and shiny June 24-27 but June 28 had an extensive mycelial coat. The

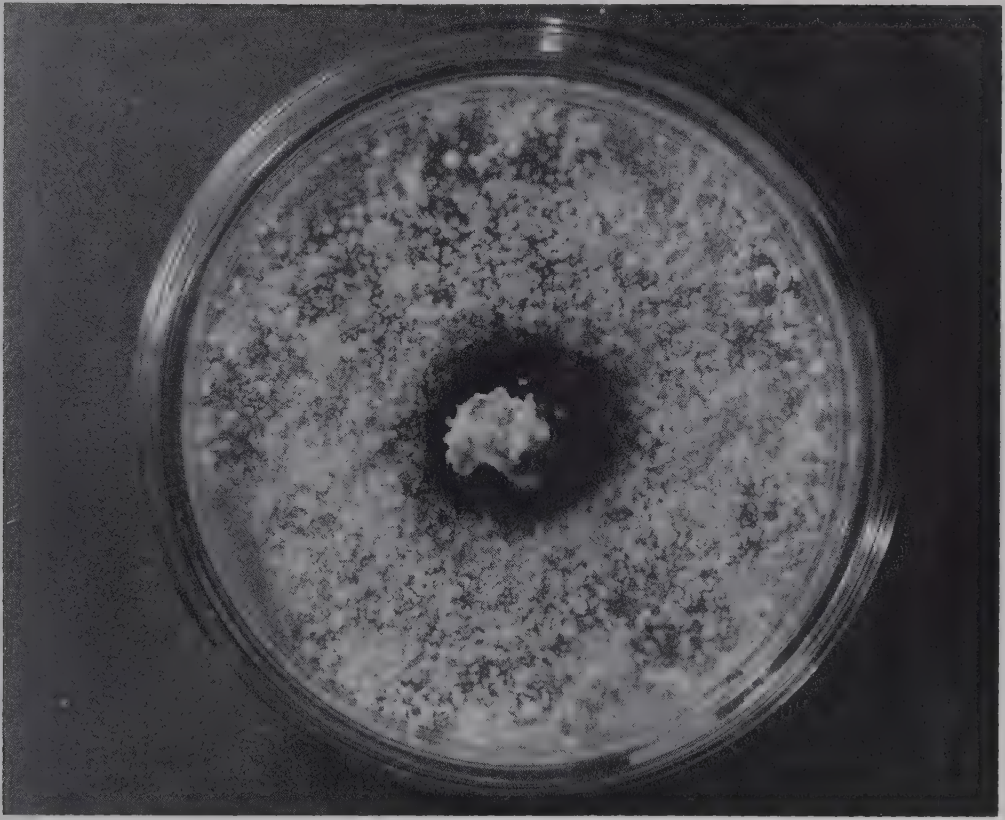

FIG. 4. Later stage of another microcosm on Sabouraud's agar in a Petri dish. The ants have removed all of the agar from the immediate vicinity of the fungus-garden, which here extends to the glass ceiling. The surrounding agar is heavily contaminated with alien fungi. Phot. Lloyd Merritts.

second larva was seen once and was smooth and shiny. A third larva about 1½ times the length of an egg was held for more than a minute by an ant while its integument was thoroughly licked. Similar behavior had been noted repeatedly. The ants were removed to a basement room (temperature 23°C) on the 28th, and on the 29th were given more sterile agar and farine to keep them during my anticipated absence. This was the third time the cover was removed.

Later Developments

Upon my return July 19 from a three-week absence (temperatures 20-24°C in the interval) an adult male was running about in the container. The male was fully mature so that it had emerged several days earlier than July 19. It is possible that the egg stage lasted about two weeks, the larval stage over three weeks and the pupal stage less than two weeks for a total of about 50 days. Temperatures were 21-33°C and much more variable than in nature. The maturing of this male indicated that the microcosm was an adequate sample of a colony from the nutritional point of view since it made the critical larva-pupa and pupa-imago transitions successfully and emerged as an apparently normal male.

Other male ants had emerged by the same time in observation nests kept nearby and made up from the merged colonies described elsewhere.

The male, a useless member of the microcosm from the point of view of contributing to the welfare of this garden and brood, on July 30 was found to lack its gaster and wings and was being carried by a worker. The gaster had probably been removed by a worker; the ant must, of course, have died soon thereafter. On July 30 the garden amounted to about two cubic centimeters in bulk and there were nine ants. The next opportunity for examination came on August 31 because of a second absence. There were now five ants alive and a much smaller garden. No brood was seen. Another ant died in early September and the garden, still luxuriant, became smaller. By October 11 it was reduced to one tiny fragment on a new site on the dark brown and contaminated agar surface over which many mites (Acarinae-Sarcoptiformes-*Tyrophagus,* det. Dr. Bohnsack) were active. By October 29 the garden was about two or three millimeters in diameter. On November 2 an ant carried a tiny pellet with a few hyphae, which appeared to represent the ultimate vestige of the garden, and the microcosm was then given fragments of garden from another nest. The ants immediately accepted them and by the next day had eaten much of the fungus. Mites were active on one fragment. On November 12 the garden was about 2 x 1 x 1.5 mm and by the 17th it was luxuriant but not one-third of a millimeter in diameter. By December 4, this having disappeared, the ants were again given a fragment from another colony and each ant immediately ran rather than walked to it. Human criteria of walking or running are applicable here since the relative rates of progression and method are comparable despite the difference in number of legs. The four ants seemed unable to develop the garden and it dwindled; mites were numerous and perhaps responsible. On December 13 they were given another fragment. This was maintained for several days only.

On January 7, 1955 the four ants were removed to another Petri dish agar plate on which a fungus developed from an *Atta sexdens* colony of Panama had been cultured since December 13. The *Atta* fungus growth was 12 mm in diameter with a central raised area 2 mm high. Four minutes later an ant defecated on the clear agar at the periphery of the fungus while another was busy tugging and cutting the fungus. A minute later another fecal droplet was deposited, this time on the periphery of the fungus itself. All ants fed upon the fungus and by January 10 they had excavated a trench in the agar at the periphery of the fungus, leaving a sharply defined fungal area 13 mm in diameter. The central area had grown in height to 6 mm. The site where the first feces was deposited was now in the cut area. Other droplets were on the fungus, which was maintained in pure culture despite growing fungal contamination on the general agar surface. By January 18 (temperatures 18-25°C in the interval) the alien fungus (*Penicillium*-type) had overwhelmed the entire surface and the ants were on the remains of the raised central *Atta* fungus.

The ants were covered with the alien spores and two were momentarily immersed in 75% ethyl alcohol to clean them. They recovered and all were transferred to a clean dish. The other two had succeeded fairly well in cleaning themselves by the next day. The two which had been bathed had evidently lost some of the water-repellent characteristics of the integument and were trapped in a film of water. They were released and seemed to recover. On January 20, however, one of the bathed and one of the unbathed died and by the 24th only one was left alive. On January 25 it had a normal garden of the *Atta* fungus on red-dyed farine which became overwhelmed by alien fungi by January 30. The ant was then transferred to a new container and given a small mass of artificially cultured fungus from another *Atta sexdens* colony. No substrate from the culture was included so that the fungus itself was the only possible source for food. The ant immediately accepted it and fed steadily, rasping it with the mouthparts, tugging at tufts of hyphae and ingesting the contents of many filaments. On February 1 red-dyed farine was added, the fungus remaining healthy, and by the 4th a normal fungus-garden had been formed with the dyed farine incorporated as substrate and hyphae were growing on it.

The garden flourished through February, the ant remaining constantly in attendance and incorporating more farine between February 15 and 22. By March 8 the garden had reached the ceiling and on the 12th both ant and garden were normal. On March 14 the ant died and the following morning it was found to have two nymphal mites on the legs and an alien fungus was proliferating from the right hind trochanter-femur joint. A large mite was on the garden, which was normal in appearance. Senility, a pathologic fungus or mites may have caused the death of the ant. It had lived alone since January 24 and on an *Atta sexdens* fungus since January 7. This ant was adult by May 15, 1954, and must have become adult by September, 1953, if not before. It was therefore at least 19 months old.

The maintenance of pure cultures of fungi in this microcosm, as in nature, appeared to be due to several factors, of which the manuring of the garden and the continual licking of the ants and the fungi may well be important. From studies on other species it was concluded (Weber 1947) "that the chemical environment created by the malaxated substrate and the fecal droplets favors the particular fungus grown by the ants." A study of the antibiotic and growth-promoting qualities of the ant saliva and feces would seem to be strongly indicated.

Pure Cultures of Fungi

In October 1953 artifical cultures of fungi secured from the fungus-gardens were started on potato dextrose and later on Sabouraud's dextrose agar. The following winter two strains of fungi were cultivated which were identified by Mr. Raymond of the Farlow Herbarium as probably *Trichoderma viride,* "an extremely fast growing and common soil organism which tends to swamp out others in cultivation." These strains were refused by the ants and were not the true ant fungus. It was not until the following spring of 1954 that cultures could be made from fresh ant gardens in the field. The usual experience was for a variety of contaminants to take over and replace the ant fungus. Commonly among these were *Aspergillus* and *Penicillium* (det. Drs. Livingston and Pope). Finally, however, a strain was secured on Sabouraud's agar which closely resembled that found in the gardens. Some of the culturing and feeding reactions are given below. Temperatures for these periods are given above under overwintering colonies and under the microcosm accounts.

By May 11 a culture of April 26, using a fragment of garden 2.5 mm in diameter, had produced a clear, superficial area 7 mm in diameter on which a few hyphae had developed. Since the remainder of the agar surface had colonies of contaminants uniformly dispersed, there appeared to be an inhibitory or antibiotic effect of the fragment. The contaminants later overran the culture. By May 18 other April 26 cultures produced bromatial growths closely similar to those found in nature.

May 11 transfers from the above cultures had produced by October 6 pure cultures of a white fungus closely similar to those being cultivated at the same time from other species of *Trachymyrmex* and *Atta* from Panama. All had generally similar aggregates or bromatia scattered through the mycelium.

When this fungus was fed to isolated ants of *T. septentrionalis* and the Panama *T. urichi panamensis* Wheeler on October 6, both species freely fed on it. The following day the northern ants were in attendance on the fungus and had defecated on it. They had clearly adopted this. This Panama species reacted similarly and maintained a garden on it through October. Ants of the subspecies *T.s. seminole* were given the New Jersey ant fungus in artificial culture on several occasions and generally accepted it.

T. septentrionalis AND OTHER FUNGI

Isolated ants in an observation nest October 15 were given access to an opened tube of artificially cultured fungus of the Panama *T. urichi panamensis.* The ants had a very small garden of their own suspended in fragments from an irregular rootlet. By October 22 the ants had found the Panama fungus, which was 29 cm distant, in the tube and were in attendance on it, the general agar surface remaining uncontaminated. This night they removed the Panama fungus, whose bulk of 18 x 13 x 1-4 mm amounted to much more than the New Jersey garden, and added it to their own garden. The two fungi were compatible and the following morning the white mycelial masses of the Panama fungus could easily be distinguished from the scanty hyphal development of the New Jersey garden. The agar in the tube formerly covered by the fungus was scored by the mandibles but remained clean. A few isolated alien colonies of fungi were developing on the general agar surface. By October 27 the ants had added farine as substrate and and they were clustered on the garden, consisting of several fragments, all suspended from the rootlet. This was their general position in the nest during the following winter. On October 29 one fragment was estimated to have a bulk of about one-half cubic centimeter and there were four other fragments of 1-2 cubic millimeters. On November 2 the garden was much smaller; it had dwindled to three tiny fragments by November 12 but was increasing by November 14. Through December it fluctuated in size, the ants using farine as substrate from time to time, and was very small on January 7 when a second tube of the same artificially cultured Panama fungus was made available. Since the ants were mostly "hibernating," they did not soon explore the tube and its fungus was still mostly intact by the 10th. The tube was removed on January 19, the ants by now having removed most of the fungus. The general cut agar surface had become slowly invaded by the alien fungi, which grew generally over the agar surface. On January 26 the garden was flourishing and had an estimated bulk exceeding one-half cubic centimeter, as three months earlier.

By March 8 the garden had become reduced to a vestige and there was a heavy Collembola infestation in the surrounding sand. The ants and garden were transferred to a Petri dish and by March 31 there remained two fragments, each about 2 x 2 x 1 mm. The ants were given more of the artificially cultured Panama fungus and immediately adopted it as before. Accidental drying of the container April 7-10 finally resulted in the death of this garden. They were then given a piece of morel-type fungus which had recently appeared in some of the same Panama ant fungus transfers. The ants consistently refused this despite the absence of food for most of a week but may have derived some nutriment from the agar base. In other experiments with the same Panamanian fungus the ants freely accepted it and cultivated a fungus garden, incorporating substrate as is usual.

When the ants were given the artificially cultured fungus from a colony of *Trachymyrmex cornetzi gatun* Weber, they at first responded by "feeling" the fungus in an indecisive manner, playing the antennal tips towards it but without tasting. It was not until the following day that the ants were actually seen to taste it and after this they fed upon it and cultivated it as their own. In a parallel experiment with this fungus and ants of the above Panamanian species there was immediate acceptance and cultivation.

The ants accepted without hesitation the artificially cultured fungus of a colony of *Atta colombica tonsipes* Santschi and in more limited experiments the result was the same with the fungus of *Atta sexdens* L., and of *Atta cephalotes isthemicola* Weber. In all cases the ants were seen clearly to eat the fungus, to manure it with their feces and to add substrate. On March 1, 1955 a female and a few workers were removed from the overwintering nest and placed without a garden in a standard container (Fig. 2). They were then given an opened tube of the morel-type *Cyphomyrmex rimosus minutus* Mayr fungus, which they soon entered although the fungus was disregarded. By March 6, however, they had cut some of the fungus into small pieces and scattered them over the general agar surface. These and similar-sized cut agar blocks remained clean of alien growths from March 8 to 10 despite contamination starting on the general agar surface, again indicating an inhibitory action of the saliva. On March 10 the female and a worker were standing beside a cluster of five eggs on the floor, one of which was 0.45 x 0.32 mm. On March 15 the ants were given an opened tube of the fungus of *Atta colombica tonsipes* Santschi which had been isolated since February 3 and had developed a dryish but luxuriant mycelium including compact bromatia. Within 3½ hours the ants had carved out and carried nearly all of the fungus a minimum distance of 17 cm to the site where the cluster of eggs and female had remained. Additional and partially contaminated fungus from the same culture was given on the 17th and within six hours they had again cut and removed much of it. The contaminated parts were discarded. By March 31 a fungus-garden of about 1.5 cc was produced which was 24 x 12 mm in diameter. During the month the daily temperature range had not exceeded 19-27°C with the great majority of hours within one degree of 23°C.

By April 5 the ants had a luxuriant garden with well-developed bromatia of the *Atta* type, more compact than that of the *Trachymyrmex*. The irregular garden was 24 x 15 x 10 mm in maximum dimensions with a bulk of about 2 cc. On April 11 four larvae, which were 1.4, 1.7, 1.6 and 1.5 mm long and 0.7-08 mm wide, were seen for the first time. By April 14 the garden was 26 x 15 x 11 mm with a bulk estimated to be about 2 cc. On April 15 two of three larvae which were visible were 2.0 x 1.0 mm and were scantily covered with a mycelium as well as imbedded in the garden, as is customary. The extreme temperatures for April 1-15 had been 20-28°C with the great majority of hours each day being within one degree of 24°C. Two callows emerged May 11.

T. septentrionalis AND OTHER GARDENS

The ants freely accepted gardens from other colonies of the same species. Whole colonies could also be successfully merged. The New Jersey ants accepted without hesitation fragments of fungus gardens of the Florida subspecies *T. s. seminole* as though they were their own.

While the ants accepted the artificially cultured fungus of the Panamanian species, they rejected fragments of the fungus garden of the same ant. Probably the total nest odor was distinctively different while the purified fungus on agar had lost this.

OTHER SPECIES GIVEN *T. septentrionalis* GARDENS

Ants of the Florida subspecies *T. s. seminole* freely accepted fragments of the New Jersey fungus gardens on several occasions.

Ants of the Panama species showed equivocal results on October 4 with fragments of gardens of the northern species. Some in one container soon explored the fragment but did not feed; others in another container at the same time did so within a few minutes. By October 6 the ants of the one isolate were still feeding on their fungus while in the other container it was ignored. On October 11 the ants were still in control and had clearly adopted it but by October 18 it had deteriorated. The same ants were then given another fragment, which was cultivated until the 27th, contamination finally overwhelming it. When the experiment was repeated November 19 in three containers with sterile agar, one fragment was maintained by the ants but the results were uncertain in the others and in all cases contamination became overwhelming in a few days.

Ants of a colony of *Atta sexdens* L. were given a fragment of a *T. septentrionalis* garden and rearranged it considerably, removing and replacing parts. They were unsuccessful in maintaining the fungus in the face of growing contamination.

On March 8 fragments of the garden of *T. septentrionalis* were isolated on damp sand in separate containers, each with a few of the nest ants. On March 10 the ants in one were replaced by several of *Trachymyrmex cornetzi gatun* which within one minute tasted the fragment and were seen crawling over it, continually feeling with the apices of the antennae. They soon had clearly adopted it and by the 15th had a normal garden about half the size of the original fragment, manuring it with their fecal droplets.

Another March 8 fragment with *T. septentrionalis* was similarly treated on March 10, the ants being removed and replaced by *Atta sexdens* workers, which had been starved since March 8. These reacted similarly to those of *T. cornetzi gatum* and were clearly seen to ingest hyphal contents. They licked the garden thoroughly. By the 12th they had eaten most of the hyphae, leaving only the farine substrate.

SUMMARY

Trachymyrmex septentrionalis McCook, northernmost of the fungus-growing ants, differs from the predominantly tropical species in being inactive in New Jersey during the period from October to March. Its fungus is capable of suspending proliferation and may then exist in the form of scattered hyphae on aged substrate. A further adaptation is the cessation of egg-laying in September and the maturation of all brood by October. In late April brood-raising may be resumed. Over-wintering colonies in the laboratory followed a similar routine despite temperatures comparable to those at which they are active in nature in the spring and fall.

In a microcosm, consisting of a few ants and a fragment of their garden on agar in a Petri dish, the ability of the ants to maintain a pure culture of their fungus, despite surrounding contamination, was striking. One such microcosm existed from May 15, 1954 to March 14, 1955. The production and maintenance of pure cultures of ant fungi may depend, in part at least, on antibiotic and growth-promoting factors in the ant feces and saliva.

Artificial cultures of the New Jersey ant fungus were developed on Sabouraud's agar and were accepted as food by the ants and cultivated by them. Ants of the subspecies *T. s. seminole* of Florida and of the Panama *Trachymyrmex urichi panamensis* reacted similarly. The New Jersey ants also accepted artificially cultured fungi of *T. s. seminole* and of Panama ants (*T. urichi panamensis, T. cornetzi gatun, Atta colombica tonsipes, Atta sexdens* and *Atta cephalotes isthmicola*).

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THE RELATION OF PHOTOSYNTHESIS BY PHYTOPLANKTON TO LIGHT IN LAKES

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In connection with limnological observations made on Bare Lake, on Kodiak Island, Alaska, it was noticed that the rate of photosynthesis by the natural population was frequently lower at the surface than at three meters' depth, especially during periods of bright sunshine, even on occasions when the phytoplankton population was uniformly distributed (Nelson and Edmondson 1955). Such surface inhibition has, of course, been observed in lakes by other investigators such as Schomer and Juday (1935), Jenkin (1930) and Manning and R. E. Juday (1941). These observations are interpretable on the basis that the saturation intensity of light for photosynthesis by a number of algae is quite low relative to the intensity of full sunlight, and moreover actual inhibition due to photo-inactivation of the photosynthetic mechanism may take place in bright light (Rabinowitch 1946, 1951; Steemann Nielsen 1949). The inhibition is of importance in connection with studies of the productivity of lakes.

For the purpose of evaluating the Bare Lake data, extensive calculations were made using published measurements of the rate of photosynthesis of planktonic algae as a function of light intensity, and of the penetration of light into water. The results seemed of general enough limnological interest that the treatment was extended and generalized, and the present paper prepared. It is believed that the matters considered here will be of use in considering regional limnology as well as in connection with the study of individual lakes.

The data on Bare Lake used in this paper were obtained by employees of the U. S. Fish and Wildlife Service. The author expresses his indebtedness to Mr. Philip R. Nelson for his cooperation in making the data available for use here. Dr. Phil E. Church, Department of Meteorology, University of Washington, made available data on radiation obtained in Seattle.

Rate of Photosynthesis as a Function of Light Intensity

Manning, Juday and Wolf (1938) presented data on the relation between photosynthetic rate and intensity of visible light for several species of freshwater algae. The organisms were suspended in water from Trout Lake, Wisconsin, and the measurements of photosynthesis made by hanging bottles of the suspensions at various depths in the lake for three-hour-periods. Photosynthesis was determined in the usual way by measuring changes in oxygen concentration in bottles exposed to light to obtain net photosynthesis, and in dark bottles to obtain respiration, permitting the gross photosynthesis to be calculated as the final difference between the illuminated and dark bottles.

The intensity of natural radiation was measured concurrently at each depth. Thus the data should be comparable with the measurements of photosynthesis made in Bare Lake by the same general method, and for this reason the Wisconsin data alone were used as the basis for computations. While much information is available on the relationship between intensity and rate for many organisms, most of the data involve light sources and culture media that are so different from natural conditions that ecological interpretation is difficult (Rabinowitch 1951).

For present purposes, three species of algae were selected from the paper by Manning, Juday and Wolf and the data placed on a relative basis by taking the maximum rate, whatever its absolute value, as 100%. The three species used are *Chlorella pyrenoidosa*, kept in pure culture, and *Anabaena limnetica* and *A. circinalis*, collected from natural populations in which they greatly predominated. A curve was fitted by eye to the data for the three species to give a presentation of the average response (Fig. 1A). With these algae, light saturation took place at an intensity that is low relative to full sunlight. There was a rather broad optimal range of light intensity giving maximum photosynthesis, above which the rate was decreased with increasing light. It would be desirable to have similar information about major planktonic species.

Further data based on extensive measurements with natural, mixed populations have been given by Manning and R. E. Juday (1941). This curve (Fig. 1A) while conforming in a general way to the average for the three single algae, does not have a broad optimal region, and falls far below the other curve in the supraoptimal region, slightly below in the infraoptimal region. The deviation may be in part an effect of difference in nutrition, since the waters of some of the lakes used were softer than that of Trout Lake, used as medium for the three algae.

In passing it should be mentioned that some freshwater algae do not show inhibition at high light intensities, in particular, certain littoral species. (Manning, Juday and Wolf 1938; McMillan and Verduin 1953.) The latter authors usually found surface inhibition in *Ulothrix,* but the intensity at which the maximum photosynthesis occurred varied considerably from one run to another; an intensity that on one occasion gave the maximum rate on another gave less than the maximum. The authors suggested that something about the spectral distribution of the light might be responsible, but it might also be suggested that differences in the photic history of the population and its nutrition may have been effective.

Throughout the following discussion, light intensity will be specified as langleys per minute. A langley, abbreviated ly., is 1 gram calorie per square centimeter (Aldrich, Wexler, Fritz, Hand, Court and Mellen 1947). Intensities given by Manning *et al.* as ergs/cm^2/min. have been converted on the basis that 1 calorie is equal to 419 x 10^5 ergs.

It should be pointed out in connection with the data used here that Steemann Nielsen has contended that the method using oxygen production in stoppered bottles gives results very much too high when production is low, but is correct when the algal population is large and production is high (1953, 1954). Steemann Nielsen's work was done with a method using radiocative carbon and usually artificial light in short runs. He proposed an explanation of the discrepancy between the two methods based on different activity of bacteria in the light and dark bottles, conditioned by antibiotic action of photosynthesizing algae. Riley pointed out objections to Steemann Nielsen's criticisms of the oxygen method (1953). The matter is under critical examination, and the results of comparative studies are beginning to appear. (Ryther 1954; Vaccaro and Ryther 1954; Ryther and Vaccaro 1954). The investigations taken as basis for the present paper used large populations of high productivity.

In discussing photochemical reactions like photosynthesis, ideally the radiation should be expressed in terms of quanta, since such reactions are proportional to the number of quanta, not the energy content in terms of calories. The energy content of a quantum is inversely proportional to the wavelength, and a calorie of red light is therefore more effective on a quantum basis than a calorie of blue light. A given intensity of light at some depth in a lake will be more or less effective depending on the spectral composition, even aside from the matter of the relative absorption by the photosynthetic pigment. Nevertheless, light that has been filtered through a meter or two of water will be distinctly restricted in its wavelength limits, and further changes are relatively small.

INTENSITY OF SOLAR RADIATION

To evaluate the importance in natural waters of the relationships being discussed, it is necessary to know the intensity of solar radiation reaching the surface of lakes from sun and sky. The most widely accepted value of the solar constant is 1.94 ly./min. immediately outside the atmosphere of the earth, but recent, unpublished work suggests that the value may actually be 2.00 (Fritz 1951; Forsythe 1954). A useful graph of the seasonal and latitudinal variations of radiation on a horizontal surface just outside the atmosphere was given by List (1951, Table 134, reproduced by Fritz, 1951).

In its passage down through the atmosphere, the light is depleted by absorption and scattering. Considerable information exists on the regional and temporal variation at the surface of the earth of intensity of total sun and sky radiation of all wavelengths.

Fritz and MacDonald (1949) published isopleths of average daily income of total radiation for each month in the United States, based on much more extensive data than the paper by Kimball (1919) which is widely quoted in earlier ecological papers. Wider geographical coverage was given by Kimball (1928). A large compilation of data for specific stations was published by Kimball and Hand (1936), and more recently (1941) Hand has presented a series of isopleths on a grid of date and time of day for the stations of the U. S. Weather Bureau at which pyrheliometers are maintained. Interpretation of Hand's isopleths should take account of the fact that each diagram of the seasonal and diurnal change in intensity of radiation represents the average of several years. Thus the maximum values shown are not the maximum possible on any given day.

Fritz (1949) published a graph of isopleths of radiation intensity as a function of air mass and mean precipitable water vapor, reproduced by Fritz (1951) and List (1951). The usefulness of the figure is extended by the paper of Shands (1949) which presents isopleths of mean precipitable water in the United States for each month.

Some interest attaches to the maximum value of total radiation to be expected at the surface of the earth on clear days. Fritz (personal communcation) writes: "Sometimes when the edge of a cloud approaches near the direct solar beam, the intensity of the radiation measured on a horizontal surface at the ground may exceed 2 ly./min. This is caused by a combination of direct radiation, plus radiation scattered downward through the edge of the cloud. This effect is usually quite transitory." According to Kimball (1919), the general maximum to be expected on a cloudless day anywhere at the surface in the United States is 1.71 ly./min. In a long series of measurements published by Aldrich and Hoover (1954) the maximum value recorded at Miami was 1.531 ly./min. and at Mt. Harqua Hale, Arizona, 1.615, at altitude of 5650 feet. Fowle (1933, Table 776) gave 1.747 ly./min. as the maximum with the sun at altitude of 82.5°, but it is not clear whether this is at sea level or at Mt. Wilson, elevation 1730 m. The daily income of radiation on cloudless days was given as isopleths for each month in the United States by Fritz (1949). Thus, we may take 1.6 ly./min. as the highest value to expect for radiation except under rare circumstances.

SPECTRAL COMPOSITION OF SUNLIGHT

Since the action spectra of plants show that only radiation within a certain range is photosynthetically active, some consideration must be given to the spectral composition of sunlight. In the literature the term "visible light" is often used where "photosynthetically active light" would be more exact. Nevertheless, "visible" is convenient to use, and as long as the terms are defined clearly, no confusion should result. The Eppley pyrheliometer, which is the instrument most commonly used for routine measurements of solar

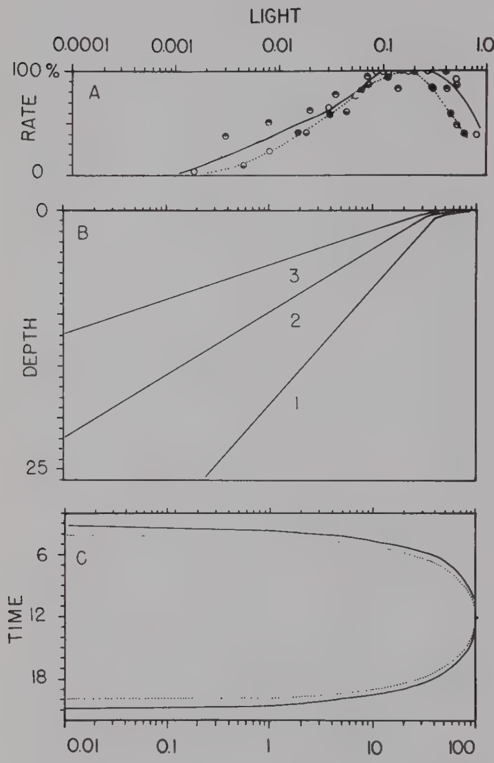

FIG. 1. A. Relative rate of photosynthesis (percent of maximum) as a function of light intensity (ly./min., visible light). Open circles, *Chlorella pyrenoidosa;* top-filled circles, *Anabaena limnetica;* bottom-filled circles, *Anabaena circinalis.* The solid line represents the average response of these three species (data from Manning, Juday and Wolf 1938). The solid circles and dotted line represent the response of a variety of natural populations (data from Manning and R. E. Juday 1941).

B. Relative intensity of visible light (percent of value just under surface) at depth (meters) in three different lakes. 1. Crystal Lake, 2. Trout Lake, 3. Lake Mendota (representative data for the lakes selected from Birge and Juday 1929). The scale numbers are shown on the bottom of Panel C.

C. Relative intensity of visible light (percent of noon value) at different hours of day. Solid line based on hourly measurements at Bare Lake, Alaska between 8 and 20 hours on July 13 and 14, 1953. Dotted line based on continuous pyrheliometric measurements on a cloudless day at Seattle, 9 July 1952 (data from Department of Meteorology, University of Washington).

radiation, is equally sensitive to all wavelengths that come through the atmosphere in appreciable intensities through the range 380 to 2900 mμ. (MacDonald, 1951.) Thus the extensive data discussed in the previous section include the large amount of infrared and the small amount of ultraviolet present in sunshine, as well as the large fraction of visible light, most of which is used by plants. The spectral composition of light reaching the earth from sun and sky is influenced by the height of the sun, amounts of water vapor and dust in the air, and other factors. It is therefore not possible to specify a single fraction, but it is necessary to ascertain as closely as possible how much of the total radiation is photosynthetically active in a range of conditions. Useful summaries of information on the spectral characteristics of solar radiation have been given by Fritz (1951), List (1951), especially Table 148, Forsythe (1954, Table 812) and especially in connection with photosynthesis, by Rabinowitch (1951).

The curves published by Kimball (1924), based on various sources, show that with clear sky and high sun, visible light is approximately half the total incident radiation. With low sun and with clouds, the proportion of visible light is even lower. The exact fraction for any given condition will, of course, depend upon what limits are taken as representing visible light. Birge and Juday, although defining red to include the range 647-800 mμ (1931, p. 397), used the limits 360-762 mμ for visible light (1930, p. 308 footnote), and evidently the subsequent Wisconsin workers whose data are used in the present paper regarded light in the same range to be photosynthetically active. It would be more useful to choose as limits those which embrace more closely the photosynthetically active light, say the range 400-700 mμ as suggested by Rabinowitch (1951).

The relative amount of radiation between various limits can be measured with a planimeter on Kimball's graphs out to 2350 mμ, which is the longest wavelength given. These graphs do not seem to take account of the strong infrared absorption bands of water vapor and oxygen (Fowle 1915). While it would be possible to make an allowance, using Fowle's data, it seems better for present purposes to make use of more modern compilations. List (1951) gives the amount of energy in various bands from 290 mμ to the extreme infrared for different air masses with a specified amount of water vapor and dust. With air masses of 1, 2 and 3, the percentage between 400 and 700 mμ is 45.2, 44.3 and 42.5%, respectively. The tabulation by Forsythe (1954) gives intensities in the range below 400 mμ, between 400 and 770, and above 770 at two localities of different altitude for different air masses with average amounts of precipitable water vapor. At Miami, with air masses of 1, 2 and 3, the percentage of vsible light is 52.3%, 51.7% and 50.4%, respectively.

Thus, for purposes of associating data on total radiation with data reported by Wisconsin authors, pyrheliometer readings may be divided by 2.0 to give the approximate intensity of the visible range. Ross and Utterback (1939) emphasized the hourly variations in spectral composition of visible daylight, and it may be expected that the infrared will vary at least as much. Nevertheless, in considering the average over a period of days, as in this paper, the factor of 2 should ordinarily be satisfactory. The greatest departure should occur when very cloudy periods are compared with very clear ones. For future work it would seem reasonable to take a more restricted range than that of Birge and Juday, perhaps using a factor of 2.2 or 2.5, corresponding to 45 or 40% photosynthetically active light. In connection with investigations of specific problems it may be necessary to determine more exactly the intensity of photosynthetically active light by measuring filtered light rather than taking a constant fraction of the total.

The measurements of light intensity at Bare Lake were obtained with a modified photographic exposure meter which had been calibrated by direct comparison with an Eppley pyrheliometer under a variety of meteorological conditions on the campus of the University of Washington. The exposure meter readings were plotted against the intensities registered by the pyrheliometer at the same time, and the line of best fit adjusted by eye. Although the photocell was not responsive to infrared, there was small enough scatter in the data so that readings could be converted to total intensity with satisfactory accuracy. Daily totals were calculated from the measurements of intensity on the basis of the length of day and the general time course of intensity during the day.

Penetration of Light into Lake Water

From the work of Birge and Juday (1929), three curves for transmission of visible light have been selected to represent a range of lacustrine conditions (Fig. 1B). While specific data on penetration of light into Bare Lake are not available, it is believed on the basis of measurements of transparency that these three curves encompass the conditions exhibited by Bare Lake from its most transparent condition to that at time of densest bloom. While the curves were selected from real cases, Crystal, Trout and Mendota lakes, no attempt has been made at detailed accuracy of transcription. The absorption below 1 meter is taken to be exponential, and the line is therefore straight on the semilogarithmic graph. The line above 1 meter is drawn as a curve to take account of the rapid absorption of red light. No account is taken of the effect of changing elevation of sun on path length, as this is not necessary for such generalized treatment. These lakes were selected because they are of very different transparency, but none has much humic stain. The mean values of Secchi disc transparency in the three lakes are approximately 7, 5 and 2 meters respectively. The use of the Secchi disc in this connection will be discussed in a subsequent section.

The spectral composition of light changes as it penetrates water (Clarke 1939). Infrared and ultraviolet are very rapidly absorbed by lake water, and only the visible penetrates in significant intensities to any great depth. For very exact work, it would be necessary to take account of the changes, but for present purposes it is assumed sufficiently accurate to consider the total energy in the active part of the spectrum. Not only were the data of Manning *et al.* taken on this basis, but the work of Jenkin (1937) showed that the procedure is sound; Jenkin found a very close proportionality between total energy and rate of photosynthesis. Apparently the effect of changes in spectral composition of light with depth is small in relatively clear waters, although it seems likely that the effect would be appreciable in stained waters.

Photosynthesis in Lakes

The curves of Panel B in Figure 1 are drawn so that 100% intensity at the surface lies just below the value 0.8 ly./min. of visible light on Panel A. By projecting from points on the main curve of Panel A vertically downward onto the curves of Panel B, it is possible to read off the depths at which the various relative rates of photosynthesis will be found. For example, under the conditions given, the maximum rate of photosynthesis will lie between 2.0 and 6.4 meters in the clearest lake, between 0.3 and 1.7 meters in the least clear.

By moving the curves of Panel B to the left, or drawing a family of parallel curves, relative photosynthesis at depth can be read for various intensities of surface radiation as has been done in constructing Figure 2, which shows lines of equal relative rate of photosynthesis down to 26 meters for various light intensities at the surface. Figure 2 was actually constructed in two steps. First, for each surface light intensity selected, a curve was drawn showing relative rate of photosynthesis plotted against depth. From this the depths at which specified rates of photosynthesis occurred were read, and these depths plotted on a grid of light intensity against depth as in Figure 2.

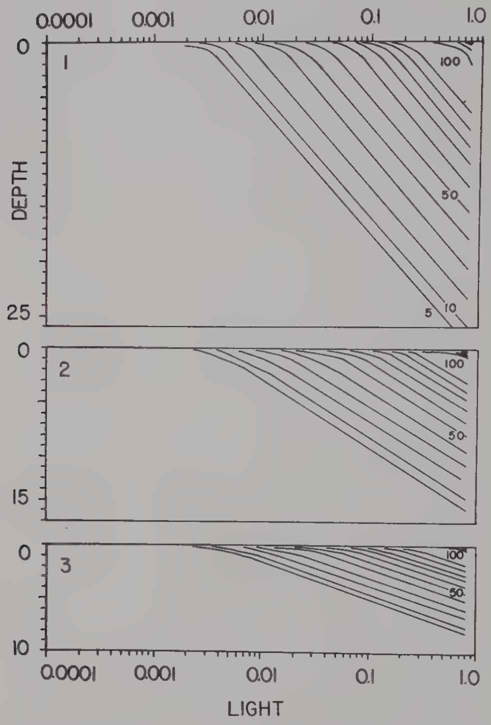

FIG. 2. Isopleths showing the relative rate of photosynthesis (% of maximum) at depths from the surface to 26 m and at visible light intensities between 0.001 and 0.8 ly./min. Each numbered panel corresponds to the similarly numbered curve in Fig. 1B. The isopleths are given for each 10%, and the bottom curve gives additionally 5%.

The general features of diagrams for the three transparency curves are similar. That is, when the surface intensity of visible light is 0.1 ly./min. the relative rate of photosynthesis at the surface is 100%, and decreases with depth. With greater light intensity, there is a finite layer in which the rate is 100%. When the surface light intensity is above 0.3 ly./min. the intensity at the surface is less than maximum, and the layer of maximum intensity lies below the surface.

The difference in the three panels of Figure 2, for the three transparency conditions, lies in the depths at which the lines of equal rate occur. The less transparent the lake, the closer toward the surface are the lines. From these data it is obvious that the inhibition can be highly significant, especially in relatively shallow lakes. To show this effect graphically in a simpler form, the average rate of photosynthesis in the entire depth of lakes of different depths has been calculated for each transparency condition (Fig. 3), at maximum surface illumination. The averages were computed planimetrically, by measuring the area under the rate curve plotted against depth, between the surface the depth indicated. Thus, on the brightest days, the clearest lake will have the average rate of photosynthesis distinctly less than the maximum possible if it is less than 5 meters deep. This critical depth is smaller in less transparent lakes. The average photosynthesis in the entire lake, 26 meters deep, was determined for a wide range of light intensities (Fig. 4).

The considerations just made have been in terms of the average relative response of three species of algae. To show what degree of departure may be expected from variations in the specific composition of population, curves for the three species could be calculated separately. Examination of Fig. 1A is sufficient to show that the same general pattern is given by all three species, although there are considerable differences at the two extremes of light intensity.

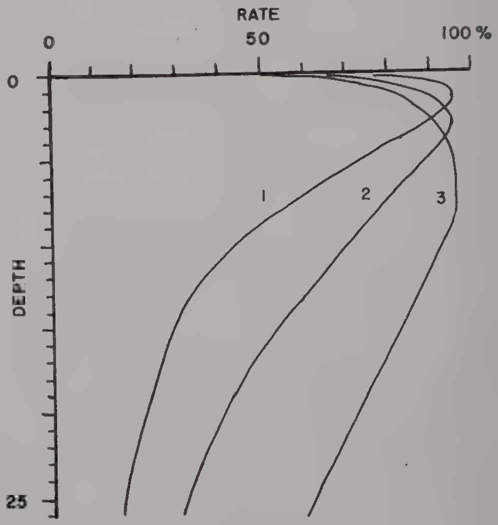

FIG. 3. Average relative rate of photosynthesis (% of maximum) in lakes of different depths when the surface intensity is 0.8 ly./min. of visible light. The three numbered curves correspond to the three similarly numbered transparency curves in Fig. 1B. The rates have not been weighted to take account of the different amounts of water at different depths.

It is thus obvious that in making measurements of photosynthesis, the vertical spacing of the suspended bottles will affect the accuracy with which an estimate of the average rate in the lake can be

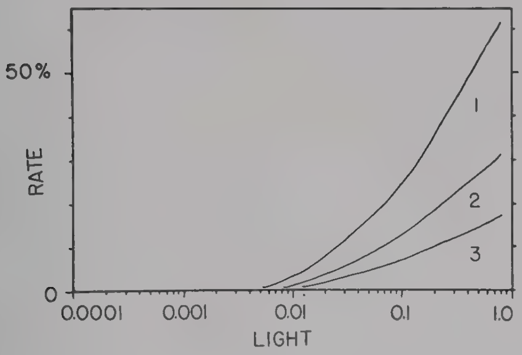

Fig. 4. Average relative rate of photosynthesis (% of maximum) in a lake 26 meters deep with various intensities of light at the surface. The three curves correspond to the three similarly numbered transparency curves of Fig. 1B.

made. If they are too widely spaced, the layer of maximum photosynthesis will be missed. In the Bare Lake investigation, measurements were made at 0, 3 and 6 meters in the lake, which has a maximum depth of 7 meters. This spacing permits reasonably close estimates of the true average except during very bright days when the lake is least transparent, when the weighted mean for the lake may be as much as 10% too low. Equal spacing of the determinations is not desirable unless the depths are close enough to give a representative sampling. If it is possible to make measurements at only a few depths, they should be placed closer together in the upper part of the lake.

It should be borne in mind that the curves of Figures 2-4 represent a high degree of idealization. It is assumed in the calculation that light is the only variable affecting photosynthesis, that the population is vertically uniform in quantity and quality, and that the medium is uniform. Thus the figures show the potential condition as it is limited by light. These conditions may often be nearly true in an unstratified lake, like Bare, or in the epilimnion of a stratified lake, but in general, any real situation will deviate from the ideal to the extent that there is vertical differentiation of the medium and of the population. In particular, differences of temperature and nutrient content will permit different degrees of realization by the population.

As a check on the general soundness of the computations, special series of measurements were made in Bare Lake in September, 1954 including 1 and 2 meters as well as the standard depths of 0, 3 and 6 (Fig. 5). The data lie very close to a curve calculated from the dotted line of Figure 1A and curve 2 of Figure 1B, using a surface light intensity of 0.3 ly./min. The actual average intensity during the period was higher, but since the days were quite variable in cloudiness, the intensity fluctuated above and below the optimum, and close agreement is not expected. The vertical pattern fits reasonably well that set by the last day of the period. It is hoped to make further checks during periods of more uniform light.

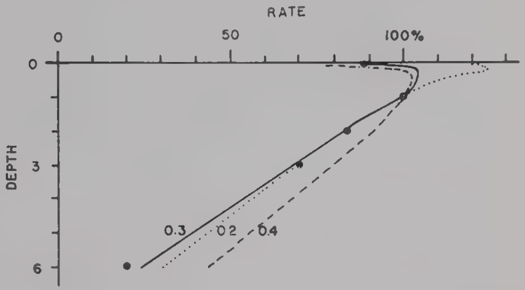

Fig. 5. Relative rate of photosynthesis (% of maximum) at depth (m). Points represent measurements made in Bare Lake September 3-7, 1954. The three lines represent the rates calculated from the dotted line of Fig. 1A using transparency curve 2 of Fig. 1B, at three values of surface light intensity, 0.2, 0.3, and 0.4 ly./min. In all cases, the rate at 1 meter is taken as 100%.

It should be pointed out that the curves presented in this paper were computed as if the light were continuous, of a specific intensity. This is not true even at the latitude of Bare Lake where the maximum day length is slightly more than 18 hours. Actually the measurements of photosynthesis reported here extended over a period of four days and nights. Nevertheless, inhibition takes place during such a large fraction of the day that the reduced light intensity at the ends of the day must be inconsequential in changing the pattern on clear days. Cloudy days may be dark enough to bring the surface intensity below optimum for the entire day. It may be expected that two runs during periods of identical mean intensity may give different rates of photosynthesis if one period includes very bright and very dark days, while the other has days of similar brightness. The resultant of a sequence of dim and bright days could be computed by numerically integrating the rates. Since the difference will be partly a matter of the rate of respiration, hence density of bacterial and zooplankton populations, no attempt will be made in this paper to assess the magnitude of the difference. Further, consideration will not be made of seasonal changes in elevation of sun and length of day beyond noting them.

Finally it is of interest to compare the results of the computations given above with conditions as they exist in lakes. A step may be made in this direction by using the dotted response curve in Figure 1A, which is based on natural populations. A set of graphs like those in Figure 2 could be prepared. Rather than duplicating that calculation, the data for Weber Lake given by Manning and R. E. Juday (1941, Table X) are used. They presented rates calculated at each meter depth for each hour of a clear August day. The data have been converted to percentage of maximum value for graphical presentation (Fig. 6). The general features are similar to Figure 2B, the differences resulting from the different shapes of the response curve and transmission curve used. The transmission was intermediate between curves 1 and 2 of Figure 1B.

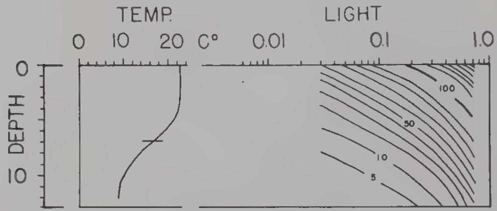

Fig. 6. Relative rate of photosynthesis (% of maximum) in Weber Lake, Wisconsin with different intensities of visible light at the surface (ly./min.). The smallest rates are calculated for 5 A.M., the highest for noon. The average summer temperature of Weber Lake is shown in the insert at the left (data from Manning and R. E. Juday 1941, Table X).

Absolute Rate of Photosynthesis

So far the discussion has been concerned with rates of photosynthesis expressed on a relative basis. Of course considerable interest attaches to the absolute rate. Manning and R. E. Juday (1941) measured the rate of photosynthesis and chlorophyll content of the phytoplankton at many depths in determinations in a series of 9 lakes. Despite the fact that the populations were presumably of diverse taxonomic composition and the lake waters were of different chemical composition, it was found that the relation between maximum rate of photosynthesis and chlorophyll concentration was remarkably close. For every milligram of chlorophyll, an average of 7.0 milligrams of oxygen was produced in an hour. The standard deviation was but 0.6, less than 10% of the mean. It would be most useful for purposes of secure prediction to ascertain in an even more varied series the limits within which this relation can be expected to hold, and to what extent departures from it may be predicted. Additional data are given by Gessner (1943, 1944) and Edmondson (1955).

The table for Weber Lake discussed in the preceding section was computed using the chlorophyll relation described above. In further computations from Table X, by Manning and Juday, allowance was made for the fact that chlorophyll from below the thermocline was less active photosynthetically than that from the epilimnetic population. This fact deserves comment. Obviously some of the chlorophyll-containing material collected below the thermocline will consist of dead algae in feces and dead or dying cells settling out from the epilimnetic population. Moreover, the photometric determination of chlorophyll may include some breakdown products of chlorophyll with a red absorption peak. Unless some technique is developed for separating chlorophyll in dead cells from that in live cells, the usefulness of chlorophyll determinations, though very great, will be somewhat limited.

Manning and Juday did not take account of temperature in making the computations for Weber Lake. The effect may not have been large, for most of the lake was homothermal (see Fig. 6 of this paper), and at low light intensities photosynthesis is independent of temperature. The basic determinations made in establishing the relationship between chlorophyll and photosynthesis were made in the epilimnion of Trout Lake, where the temperature varied only 2° from 22.5°C (1941, p. 366). Lower temperatures were found only at very low light intensities. Schomer and Juday (1935, p. 181) state that in their work, respiration varied little in the range of temperatures experienced in Crystal Lake (11.3°-22.9°C), but this condition has not been found by others (Anderson 1954). The role of temperature adaptation in phytoplankton remains to be studied thoroughly (*cf.* Steemann Nielsen 1954, p. 316). It is still to be determined whether the relative lack of effectiveness of chlorophyll from below the thermocline is in part a matter of temperature and perhaps light adaptation.

Chlorophyll is not the only base to which photosynthesis may be referred, although it is probably the most direct. Verduin (1952) has shown that rate of photosynthesis bears a reasonably close relation to plant volume in a wide variety of organisms, but whether the relation will be of predictive use in lakes remains to be seen.

Photosynthesis at Different Times of Day

It is of interest to calculate the depth distribution of photosynthesis at different times of day

The curves of Figure 1C, showing the relative intensity of light with the noon intensity taken as 100%, are based on measurements at Bare Lake (Lat. 58° N) and Seattle (Lat. 48° N) during cloudless summer days. There is some doubt about the exact values when the intensity is less than 1% of the noon value. The lines for low intensities have been drawn to take account of the fact that at the moment of sunrise intensity is approximately 0.5% of the noon intensity (Kimball 1916). For both curves, it is seen that the surface intensity is at or above the lower optimal value for about 85% of the time between sunrise and sunset, and will be above the upper optimal value for about 73% of the same time. These proportions hold approximately for a wide range of latitude and time of year.

Compensation Depth

The depth at which photosynthesis is just balanced by respiration, so that there is no net change in oxygen concentration, is the compensation depth. Although it is usually defined in terms of oxygen balance, the chief importance of the compensation depth is in determining the part of the lake in which there can be a net photosynthetic increase in the amount of organic matter. Associated with it is the compensation intensity (or compensation point) of radiation. In dealing with a natural population, the most useful concept of the compensation depth and intensity are those associated with the 24-hour day. Naturally the compensation depth changes from day to day as the incident radiation changes with atmospheric conditions. The compensation intensity has a clear physiological meaning in connection with a unialgal, bacteria-free culture. With natural populations which contain heterotrophic organisms, the ecological significance is equally clear, but the situation is more complex and less regular. The compensation intensity is higher in a natural population than in one free of heterotrophic organisms, since the production of oxygen by algae must take care of the respiration by animals and bacteria as well as by themselves.

For *Chlorella,* the compensation intensity is about 0.0014 ly./min. of active light (Rabinowitch 1951). For a marine diatom in overnight determinations, Jenkin (1937) obtained 0.00217, but the cultures were not completely free of bacteria. Schomer and Juday, using cultures of two species of algae, not bacteria-free, obtained values from 0.004 to 0.010 in three relatively lightly colored lakes. The rates of photosynthesis associated with these four values are 6, 14, 24 and 42% of the maximum value, according to the solid curve in Figure 1A. In a highly colored lake the values were much higher. Although the degree of bacterial contamination is not known, the larger values may be more represenative of natural populations and the smaller more representative of populations with a high proportion of photosynthetic organisms. Respiration may amount to 5-10% of photosynthesis in exponentially growing, bacteria-free *Chlamydomonas* (Ryther 1954). Thus, the maximum possible mid-day compensation depth is given approximately by the 5% isopleths in Figure 2, but ordinarily it will be much shallower. The corresponding 24-hour compensation depth will depend on the length of day and character of the population.

For natural populations, how much higher the compensation intensity will be will depend upon the proportion of the extra respiratory demand by the nonphotosynthetic organisms. Ideally, one could determine this on the basis of illuminated bottles in which the oxygen concentration did not change in a day, but practically this intensity is not now open to exact measurement since a great number of bacteria will ordinarily grow on the glass walls of the bottle during the measurements, and make a false increase in oxygen demand. Possibly the true value of the compensation depth of natural populations can be approximated by techniques involving the addition of various known areas of glass to a series of bottles, permitting the effect of the periphytic bacteria to be evaluated.

Penetration of Light as Estimated by Secchi-disc Transparency

To make computations of the sort discussed for a specific case requires specific information on penetration of light. Often equipment is not available as at Bare Lake where all equipment must be flown in by airplaine. It is then necessary to use approximations or abandon efforts to work with the kind of problem under consideration beyond making measurements for purposes of description. Since these matters are of current interest and importance in limnology, an attempt should be made to determine whether useful approximations can be made. Specifically, one needs to know in a given case which of the three transparency curves (Fig. 1), or what intermediate condition to use. If a basis of choice can be made short of making the elaborate, direct measurements themselves, work in this field will be greatly facilitated.

The main question is whether a penetration curve can be derived from the transparency, perhaps supplemented by other measurements. It has been shown that a loose hyperbolic relation exists in the sea between Secchi-disc transparency and the average extinction coefficient k for visible light. The relationship may be formulated as $k = \frac{C}{D}$ where C is an empirically determined dimensionless constant of value 1.7, D is the Secchi-disc transparency, and k is the extinction coefficient per meter as defined by the relation $I_d = I_0 e^{-kd}$ in which I_0 is the intensity at depth 0, just under the surface, and I_d is the intensity at depth d (Poole and Atkins 1929; Clarke 1941). The same numerical relationship would not be expected to hold for water highly stained with humus, and indeed it does not (Anderson 1954). Nevertheless, it may be expected that a similar hyperbolic relation holds, and that the value of the constant C might be adjusted for different conditions of stain and perhaps plankton and silt.

Juday and Birge (1932, 1933) showed that the Secchi transparency is affected both by particulate matter in suspension and by stain, particularly the latter. Thus, in one lake the transparency may vary during the year if the phytoplankton population or solt content varies, and in a series of lakes of uniform suspended matter the transparency will vary greatly depending upon the amount of dissolved stain. Table 1 of the 1932 paper gives data on transparency, color (U. S. G. S. Scale), and the depth at which particular fractions of the surface intensity occur. There is a fairly close and nearly linear relation between transparency and, for example, the depth at which the 1% value occurs. The lower transparencies are in lakes with more color. For any transparency, there may be a range of depths. For instance, in the two series in Crystal, the transparency was 13.0 m, and the depth at which 1.0% of surface intensity was measured was 18.0 and 14.5 m. The latter measurement was associated with a large population of *Dinobryon* in the lower water. Many measurements of transparency and transmission at different times in Lake Mendota are summarized by Birge and Juday (1929, Fig. 9). The trend is clear, but scatter is high. Nevertheless, in view of the effect of plankton on transparency, it is reasonable to suggest that for each value of transparency, scatter could in part be accounted for by plankton, and a family of curves drawn across Birge and Juday's graph which would permit a usable estimate of transmission from the measured transparency. The relationship of Secchi transparency to particulate matter measured as dry weight of seston and to stain measured on the U. S. G. S. scale are both approximately hyperbolic, with small differences in the low range being associated with large differences in transparency.

Since the quantity of plankton may affect the relation between the variables under consideration, it may be suggested that the matter needs further investigation with attention directed to the specific points discussed. It is necessary to consider whether the U.S.G.S. color scale is adequate; it probably is not. More likely, the Forel-Ule scale, or some modification of it may be more useful, since in a lake without visible stain, the color of light returning to the eye from the Secchi disc at half the transparency depth will vary from blue through various shades of green depending on the amount and character of the plankton.

In view of the change of slope of the curve for total light intensity in the upper meter or two, computation of an average transmission coefficient, k, is insufficient, but at least it should be possible to draw up a family of curves similar to that in Figure 1B, but more closely spaced. Each curve would correspond to a range of measured features that affect penetration of light. Heavily silted and heavily stained waters may have to be left out of consideration, but it may be found that the relations are close enough in lightly colored waters that a usable relation may be found between transmission and transparency, U. S. G. S color, and Forel-Ule color. Of course for specific investigations direct measurements of light at depth will often be indispensable, but for purposes of generealization, further attention must be given to the relations just discussed.

Statistical Correlaton between Photosynthesis and Light

Riley (1940) and Anderson (1954) have investigated the statistical relationship between light income and measured photosynthesis by natural populations in lakes. They found low partial correlations between light and photosynthesis of natural populations in surface water, and obtained higher partial correlations only when considering the entire depth of the lake. Such a situation is understandable on the basis of the relationships discussed here; on clear days, maximum photosynthesis at the surface will be associated with a wide range of light intensities, and rates can vary between 100 and 50% with either high or low light intensities (Fig. 1A). Thus the light income during the periods of measurement can vary greatly without having directly related variations in photosynthesis. Only during cloudy days when light is below optimal most of the time may a direct correlation be expected.

When measurements are made throughout the trophogenic zone of a deep lake, higher correlations will be expected, for surface inhibition is to some extent more than compensated by increase in deeper water. This effect is well shown in Bare Lake by the rate at the three depths 0, 3 and 6 meters during periods of different light intensity (Fig. 7). In general, the highest surface rates occurred during the periods of lesser light income.

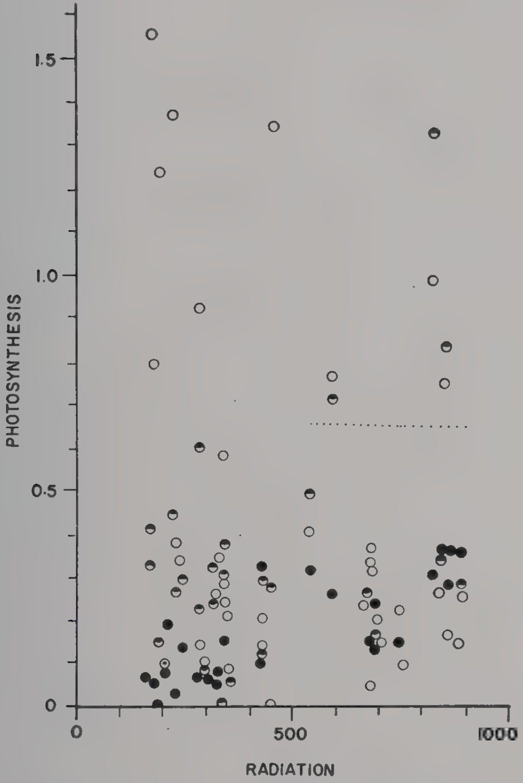

Fig. 7. Measured rates of photosynthesis in Bare Lake at three depths as a function of *total* radiation. Photosynthesis is given as mg of oxygen produced per day. Radiation is given as ly./day. Open circles represent measurements made just under the surface, half-filled circles at 3 m, filled circles at 6 m. Data for 1953 with a few sets at low light intensity from 1952. The points lying above the dotted line represent measurements made just after the second fertilization. Note that both rates are given on a daily basis.

During the brighter periods, the lowest rate in each series was at the surface, with either the 3- or the 6-meter rate being the highest. The points which lie highest at relatively high radiation incomes are for the period immediately after the second fertilization when the population was larger than it had been earlier. The rate at 6 m shows a distinct tendency to rise with increasing light income.

Population Efficiency

In Bare Lake, Nelson and Edmondson found that the maximum efficiency, or fraction of total radiation used in photosynthesis by the whole lake occurred during periods of relatively low light income (their Fig. 4). In relation to the present discussion, it is of interest to compare the absolute rates of photosynthesis with daily light income, as in Figure 8 which additionally shows the efficiency by means of isopleths. There is obviously no or little correlation in Figure 8 between daily light income and daily rate of photosynthesis. In the range 150-900 ly./day, the data show hardly any trend, except for a slight tendency toward inverse correlation.

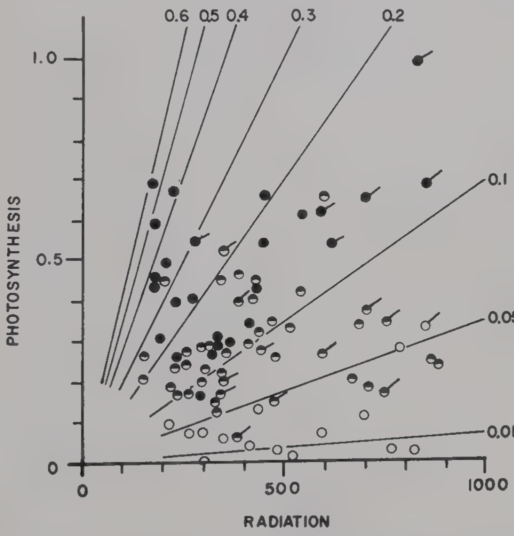

Fig. 8. Measured rate of photosynthesis in Bare Lake as a function of *total* radiation. Photosynthesis is given as average mg. of oxygen produced per day for three depths, weighted for the amount of water in the lake between the depths of measurement. Radiation is given as ly./day. Open circles represent measurements made before the first fertilization each year, half filled circles those after the first fertilization, filled circles those after the second fertilization. Circles with tails show the first three measurements made after each fertilization. The lines radiating from the origin show the efficiency of the lake population as percentage of the total energy at the surface corresponding to the energy equivalent of the rate of photosynthesis. This graph corresponds to Fig. 4 of Nelson and Edmondson (1955). Note that both rates are given on a daily basis.

Obviously, not all the variations in photosynthesis can be attributed to light. With any given light intensity, the photosynthetic rate will depend upon the quantity and kind of phytoplankton, its condition, and the condition of the environment. Inorganic nitrate and phosphate fertilizers were added to Bare Lake on several occasions. The points for the time before the lake was fertilized as a group lie low. Those after the second fertilization of a given year lie high, and those after the first fertilization are intermediate. It is intended to publish a full analysis of the variations in photosynthesis, light, population and nutrition in Bare Lake after more data have been obtained.

It has been shown that light inhibition in *Chlorella* is relieved by the presence of a large concentration of carbon dioxide (Emerson 1935). It would be of considerable interest to know how general this effect is, if it operates under natural conditions, and if other substances of less direct significance in photosynthesis might be similarly effective.

CONCLUSIONS

When productivity is considered on a regional basis the geographical distribution of photosynthetically active light is of basic importance. To understand the way in which the variations are effective, it is necessary to study the details of the photosynthetic response of populations to light intensity, and the variations of intensity with regard to geographical postion, time of day, season, and depth in lake. In particular cases it may be possible to simplify the computations from those presented above, but this must be done in the light of detailed knowledge.

The relationship of photosynthetic rate to light intensity, as summarized in Figure IA, is of use in evaluating the effect of variations of light on photosynthesis. Plainly, much of the time, photosynthesis in the upper part of lakes will be held in check by intense light. Light can vary over a wide range of intensity without proportional variations of photosynthesis.

Within a lake, the vertical variations in potential rate will be largely determined by the surface intensity and transparency. Variations in distribution of population, nutrients and temperature will modify the basic pattern. In deep lakes and the ocean, surface inhibition by intense light will largely be compensated by increase in deep water, a point emphasized by Steemann Nielsen (1954). Ponds and many lakes are shallow enough that the depth of inhibition is a significant fraction of the maximum depth, and the average rate under a unit area may be reduced as the surface intensity increases above the optimal value.

An additional factor which must be taken into account is the effect of stratification. If the epilimnion is thicker than a certain critical depth, the phytoplankton population will be unable to grow. The value of the critical depth depends in part on surface illumination (Sverdrup 1953).

In view of the regularity of the intensity-time curve (Fig. 1C), knowledge of the length of day and noon intensity is sufficient to establish the main facts about photosynthetic potential on days of no clouds or uniform cloudiness. It would be quite easy to calculate the fraction of the day during which photosynthesis was proceeding at maximal rate or was inhibited, and during which it was more nearly proportional to light. Seasonally, these fractions may change greatly because of general cloudiness and rain, or low solar elevation. Evidence has been presented by Lund (1949) that growth of *Asterionella formosa* is held in check in the English Lake district during the winter by low light intensity, at least primarily. Even though a day must be quite dark to reduce the rate of photosynthesis at the surface below the maximum, the rate at depth may be greatly reduced on dark days as compared to bright days (Fig. 2).

Plainly much of the time over large areas, potential photosynthetic production in the upper water of lakes will be reduced by intense illumination. Only in moderately deep lakes or untransparent lakes can we expect anything like a proportionality between the surface illumination and average photosynthetic potential; for such lakes the illumination isopleths presented in the meteorological papers discussed may be of direct use in interpretations of geographic variation of photosynthetic potential as it is set by light.

Of course nothing in this discussion is to be taken as a lack of recognition of the importance of geographic variation in other factors known to affect productivity, such as nutrients and temperature, but it is obvious that even with the most favorable natural media and temperatures, photosynthesis will not proceed without light, and too much light will be inhibitory. The discussion has been limited to phytoplankton, but it will be necessary to work out similarly the photosynthetic relationships of rooted plants and periphytic algae to make a complete description of a lake.

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ADAPTIVE DIFFERENCES IN WATER-HOLDING CAPACITY IN AN INTERTIDAL GASTROPOD

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Introduction

Desiccation is one problem faced by marine intertidal animals. Many species are only sufficiently adaptable to withstand a limited range of exposure and consequently occupy a restricted intertidal zone. Others have a relatively wide vertical distribution and are faced with a wider range of exposure conditions. The aspidobranch gastropod *Acmaea limatula* Carpenter possesses such a distribution along the Southern California coast. Individuals at the lowest level of the species' range are continually submerged and are not faced with the problem of drying. The highest individuals are found approximately four feet above zero datum (taken as the mean of the lower of the two low waters of each day; extreme tidal range in this region, approximately —2 to + 7.0 feet) and are submerged about fifty per cent of the time. Although the animals are motile and are able to move a number of feet in a day, the nature of the beach (Palos Verdes, California) prevents any large interchange between shore levels.

The present investigation shows that there are certain differences in the size of soft parts and the volume under the shell which are correlated with the intertidal position of the animals. These differences directly determine the amount of water held between the shell and soft parts.

The data presented below are a part of a study on ecologically significant differentiation within the species. The remainder of the findings on differences in heart rate, gonad size and spawning time will appear elsewhere.

Methods

Soft parts and shell were separated by cutting the attachment muscles close to the shell. Each was damp-dried on absorbent paper towelling and weighed individually until successive readings were identical. In this way water retained in the mantle cavity of the intact individual did not enter into the weight measurements.

Shell volume measurements were accomplished by supporting an inverted shell in a plasticene mount. Then benzene (approximately one-third the surface tension of water at 20° C.) was introduced into the shell from a one cubic centimeter syringe until the meniscus was level with the shell rim. A white background card facilitated reading the meniscus level. An average value of three to five readings was computed.

Shell thickness was obtained with the use of a micrometer.

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Results

Eighty high-level and sixty-five low-level individuals were weighed and the shell weight as a function of the wet weight of soft parts is plotted in Figure 1. The individuals were randomly picked with respect to shell weight; an effort was made to obtain representatives of each size class within the limits shown.

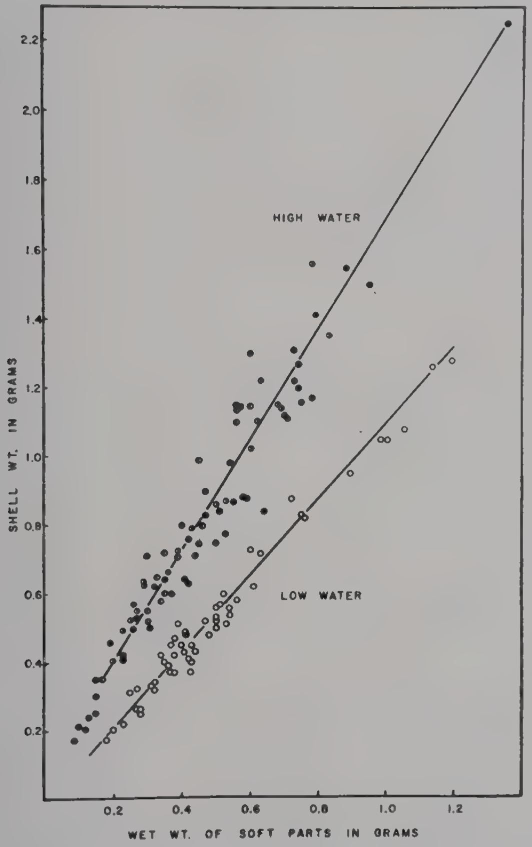

FIG. 1. Relation between shell weight and wet weight of soft parts in high- and low-level *A. limatula*. Each point represents one individual. Measurements made in June 1954, when size of gonad was not significantly different in the two groups. High-level animals collected from three sites along the Palos Verdes, California, coastline. Low-level animals collected from two.

From the data it is apparent that the heaviest shells for any given wet weight of soft parts are found among the high-level individuals. The linearity of the curves suggests that the ratio of shell weight to wet weight of soft parts is relatively constant for a given population. An approximate shell weight to wet weight ratio is 2:1 for high-level animals as contrasted with 1:1 for low-level animals.

When the fluid volume held by the empty shell is measured and plotted against the wet weight of soft parts, the curve for the high-level group lies above that for the low-level group (Fig. 2).

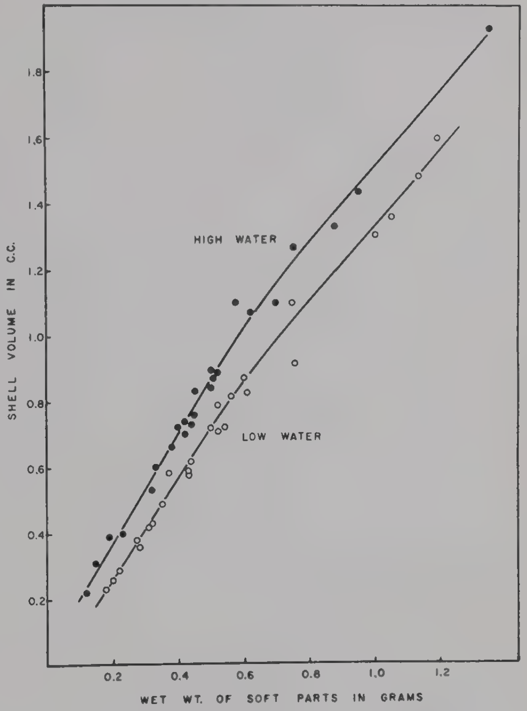

FIG. 2. Relation between shell volume and wet weight of soft parts in high- and low-level *A. limatula*. Each point represents one individual. Volume is the amount of fluid (benzene) that a shell can hold.

Therefore, the shell of a high-level limpet holds more water per given wet weight of soft parts. Up to a point the ratio of the shell volume to wet weight of soft parts is relatively constant for a given group. Above approximately the 0.6-gm category the slope of the curve changes in both populations, but the scarcity of points does not permit a more definite statement.

From the preceding data (Figs. 1, 2) on the relationship of shell weight and shell volume to body weight, an idealized curve has been derived expressing the relationship between the weight and volume of a shell for any given weight of soft parts (Fig. 3). A comparison of two shells of equal weight shows that a low-level shell can hold a larger volume of fluid than a shell from high level. Conversely, shells of equal volume show the high-level shells to be heavier.

Shell thickness of twenty-five shells from high- and low-level was measured with a micrometer. Using an area 2 mm posterior to the apex, high-

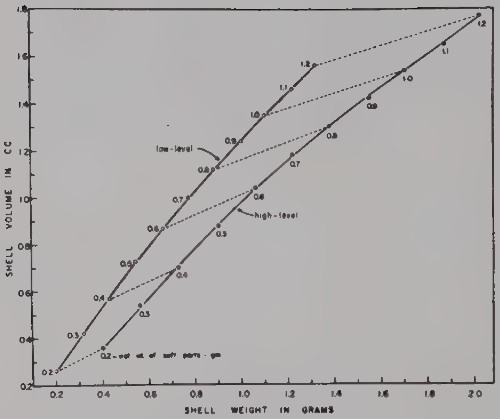

FIG. 3. Relation between shell volume and shell weight for any given wet weight of soft parts from 0.2 to 1.2 gm. Points derived from curves in Figures 1 and 2.

level shells were found to average forty-one per cent thicker for any given shell length from 21-33 mm. Therefore, when comparing shells of equal weight, high-level shells hold a smaller volume of fluid because of their greater thickness.

Although high-level shells hold less fluid than low-level shells of equal weight, the smaller absolute size of the soft parts of the high-level organism more than compensates for the difference (Figs. 1, 2). Therefore, there must be a larger water space between the shell and soft parts in high-level limpets. On the assumption that the specific gravity of the soft parts is equal for both high- and low-level animals and approximates 1.00, the wet weight of soft parts was subtracted from the volume of fluid held by the empty shell and plotted as in Figure 4.

With increasing size, the extra-visceral space (the volume under the shell minus the volume of soft parts) does not increase proportionately for either group. When the extra-visceral space is expressed as a percentage of body weight (inset, Fig. 4), it can be seen that there is a decrease with increasing size among high-level limpets. Low-level animals show an increase to a high value for an animal of approximately 0.6 gm and then a decrease. The difference between the groups decreases rapidly with size and levels off. A small high-level animal has a proportionately greater extra-visceral space, relative to its body weight, than either (1) a larger animal from the same habitat or (2) an animal of any size from the low-level habitat.

DISCUSSION

Russell (1907) comparing shells of high- and low-water *Patella vulgata,* found that high-water limpets were at all adult stages higher spired than low-water limpets. Orton (1929, 1933) confirmed this finding and showed, in addition, that shells of high- and low-water *P. vulgata* differed in the relation between shell thickness and weight and other mensural characters. Shells of high-water animals were heavier, thicker and higher spired.

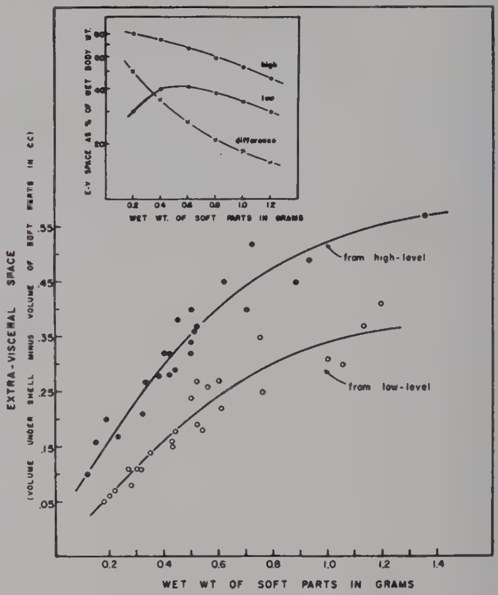

FIG. 4. Relation between extra-visceral space (shell volume minus the volume of soft parts) and wet weight of soft parts in high- and low-level *A. limatula.* Each point represents one individual. Inset—relation between extra-visceral space as per cent of body weight and the wet weight of soft parts. Points derived from the fitted curves.

Wagge (1952) has considered some factors in the diet which may influence shell thickness in molluscs. He suggests that the size and thickness of a snail's shell may depend as much on the snail's rate of growth as on the amount of calcium present in the diet (see also Moore 1936).

Orton suggested that the higher spire of high-water shells was the result of a mechanical process of deformation. High-water *Patella,* since they are exposed to desiccating conditions to a greater degree than low-water individuals, were supposed to contract the foot and mantle to present the edge of the shell with close apposition to the substratum. The shell, laid down *in situ,* assumes a smaller ellipse than the shell of low-level animals with extended mantle. High-level shells have thus a taller spire and a narrower base. By transplanting high-water animals to rock pools Moore (1934) experimentally supported Orton's theory.

With subsequent growth the transplants widened the shell angle by laying down a pronounced ledge all around the base of the shell. Hatton (1938), however, transplanted *Patella vulgata* from the 10-m to the 6.5-m level and could not discern a change in shell shape.

Observations and measurements on *Acmaea limatula* have confirmed the results of others with regard to the greater weight and thickness of high-water shells. When the volume under the shell was measured it was found that high-level shells, when compared with low-level shells of equal weight, hold less fluid. Since high-level animals are subject to conditions of desiccation, the volume differences, at first sight, would appear to be non-adaptive. One would imagine that the water-holding capacity would differ from that of low-level animals in a direction inclining towards "better fitness" for the habitat. Analysis of shell and soft parts reveals that this difference is compensated for by the smaller size of soft parts in high-level animals (Fig. 2).

Shell and volume measurements were deliberately made in June when the size of the gonad was similar in the two groups (Segal 1955). But gonads of high-level individuals are of insignificant weight from approximately December until April. These months correspond to that period of the yearly tidal cycle when high-level limpets are exposed during the hours of greatest insolation in this area. Therefore, the extra-visceral space may be presumed to be considerably larger in high-level animals exactly at the time when an extra reservoir of water is most needed.

Shotwell (1950), working on the Oregon coast, reported that smaller individuals of *Acmaea scutum* and *A. cassis* (= *pelta*) occur throughout the intertidal range while larger individuals are confined to the lower portions of the range. *A. limatula,* on the contrary, does not possess a size distribution as reported by Shotwell. All sized animals were found at all intertidal levels; in fact, some of the largest shell volumes were found at the highest points of the range. *Patella vulgata* has a pattern of distribution in relation to size; the smaller individuals are found lower in the intertidal zone (Jones 1948; Das and Seshappa 1948; Lewis 1954). From the work of Abe (1931), who found that small indviduals (shell weight plus the weight of soft parts) of *Acmaea dorsuosa* possess a relatively greater amount of "stock water" than larger individuals, Shotwell concluded that his size distribution was based upon the water-holding capacity of the animals. However, the water-holding capacity is not determined by the shell volume alone, but rather by the shell volume minus the volume of soft parts. Small, high-level *A. limatula* do possess a relatively greater amount of extra-visceral or "stock water"; below a certain size, small, low-level *A. limatula* do not when each is compared with the larger limpets from the same habitat. Large high-level limpets possess both absolute and relatively greater extra-visceral spaces when compared with animals of any size from low-level (Fig. 4). Therefore, it is evident that the water-holding capacity of a given limpet cannot be predicted from measurements of the shell volume alone.

Though the osmotic relations of *A. limatula* are not known, marine molluscs in general are in osmotic equilibrium with the surrounding sea water (Krogh 1939). During exposure, high-level *A. limatula* are presumably in equilibrium with watery microhabitat under the shell. Evaporative water loss from this extra-visceral space must be granted under natural conditions. Investigation has shown that as the concentration of the microhabitat (under shell) water rises the soft parts lose water to the medium. After a period of exposure high-level animals lost two to five percent of the body weight, depending upon the size of the animal, although water still occupied the extra-visceral space. Submergence in sea water for twelve hours returned the body water to normal, *i.e.* to a level approximating that of continuously submerged low-level animals. If the larger extra-viseral space means larger water volume while the area at the periphery available for evaporation is the same, then the percentage water loss is less in the animals with the larger volume of extra-visceral water. This is of adaptive significance in the high-level animals which characteristically possess the larger extra-visceral space.

It is of interest in this connection that when transplanted to the high-level habitat, low-level animals migrated out of the region of direct insolation and settled in damp protected sites beneath the boulders, although the resident limpets were scattered over the tops of the boulders (Segal 1955).

A more secure basis for the conclusion that the difference in water-holding capacity is adaptive requires reliable data on toleration of osmotic stress. We need to know the magnitude and duration of a stress that can be tolerated without difficulty or forcing important behavioral reactions. We also need to know whether such stress is ever encountered in nature.

Acknowledgments

The studies on microgeographic variation within the species were pursued under the guidance of

Dr. Theodore H. Bullock. I wish to thank him for his many helpful suggestions and a critical reading of this manuscript.

SUMMARY

High- and low-level *Acmaea limatula* differ in the relation between shell and body weight, and in shell volume and the size of the extra-visceral space. High-level shells are thicker and heavier for a given weight of soft parts. Although high-level shells hold less volume than low-level shells of the same weight, the smaller body more than offsets this. Therefore, high intertidal individuals, living under desiccating conditions, have a larger water space between the shell and soft parts.

It is suggested that the greater water-holding capacity of high-level animals is adaptive but only if a larger extra-visceral space means a larger water volume. Given equal area for evaporation (at the junction of the shell and substrate) it must be assumed that either (1) the entire extra-visceral space is filled with water, or (2) the proportion of air is constant for a given size space. The percentage water loss would then be less in those animals with the larger extra-visceral space.

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REACTION OF CILIATES TO ENVIRONMENTAL FACTORS

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INTRODUCTION

Ciliates are of cosmopolitan distribution and are restricted solely by ecological factors. Because of this similar habitats have similar faunas, and special habitats, such as sewage plants, have a characteristic fauna. For the most part, however, ciliate species are widely distributed throughout soil, fresh water and marine habitats, although not always occurring regularly in the same habitat. Both in nature and in the laboratory there is normally a succession of forms, or sequence, sometimes characterised by rich blooms of some species and often ending with the death or disappearance of all active forms.

Although many ecological factors, and especially food, have been suggested as the cause of these protozoan sequences, the wide tolerance of most species and the lack of any positive correlation or experimental evidence have rendered such explanations unsatisfactory, without further proof. Species are often classified according to the scheme of Kolkwitz and Marsson (1909) by their tolerance of organic pollution, but such classification, while of value, does not distinguish the specific environmental factors which affect the ciliates. For this reason, Lackey (1938), after a full discussion of the problem, concluded that species should not be classified ecologically until their range of tolerance of environmental conditions is known.

This paper is concerned with relating the ecology of ciliates and their culture history to their response to specific environmental factors, such as bacteria, pH, anoxia and high carbon dioxide tensions.

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In correlating the ecological and experimental evidence of different workers some difficulty is experienced in determining the species concerned, for not only has there been considerable systematic revision over the last half century but complete uniformity has not yet been attained and the identity of some of the earlier material can only be guessed at. Where there is doubt I have used the original nomenclature of the author, but where the identity is comparatively certain I have employed the currently accepted nomenclature so that experiments and observations on the same ciliate may be compared without confusion. An obvious case is *Tetrahymena pyriformis,* for which *Glaucoma pyriformis* and *Tetrahymena geleii* were commonly employed synonyms; *Colpidium campylum* Hetherington is also a synonym of *T. pyriformis* and is distinct from *C. campylum sens. str.* (Corliss 1952).

The ciliates used in my experiments were obtained from soil, beech litter, and fresh water samples from lagoons, reservoirs and streams.

CULTURE EXPERIMENTS

Growth in different media

The simplest method of establishing a soil culture is to add water to the soil, keeping the culture in a closed dish or test tube to prevent evaporation and contamination. The second method is to use an enriched culture. Sandon (1927) found that different culture medias gave rise to different faunas and this was confirmed by Dixon 1937). She found that with different media (peptone agar, soil extract and hay infusion) the peptone favoured specialized species of bacteria and protozoa, where as soil extract permitted growth of many species in small numbers.

The following media were prepared.

(*a*) Soil extract: this was prepared by steaming soil (100 grams) in a steam sterilizer for an hour and a half in a litre of water. The water was subsequently poured off and diluted before use.

(*b*) Peat extract: similarly prepared from initially dried peat.

(*c*) Yeast extract: similarly prepared from commercial bakers' yeast.

(*d*) Peptone: de Witte's peptone in concentrations of 5%.

(*e*) Yeast extract-peptone-glucose: 1% yeast extract, 2% peptone, and ½% glucose.

The various media were placed in Syracuse watch glasses and inoculated with protozoa from a flourishing beech litter culture. The species occurring in the various culture media were recorded and their approximate abundance. These are given in Table I.

TABLE I. Growth of protozoa in different media

Protozoan species	(*a*)	(*b*)	(*c*)	(*d*)	(*e*)
RHIZOPODA					
Biomyxa vagans	x	x*	.....	.....	.....
Mayorella vespertilio	x	x	x	.....	.....
Trichamoeba sp.	x	x	.....	.....	.....
CILIATA					
Spathidium sp.	x	.....	.....	.....	.....
Enchelys sp.	.....	x	.....	.....	.....
Chilodonella sp.	x	.....	.....	.....	.....
Trichopelma sphagnetorum	x**	x**	x*	.....	x
Colpoda steinii	x*	x*	x**	.....	x***
Colpoda cucullus	x	x	x	.....	.....
Colpoda inflata	x	x	x**	.....	x
Colpidium sp.	x	x	.....	.....	.....
Cyrtolophosis mucicola	x	.....	.....	.....	.....
Cyclidium glaucoma	x	x	.....	.....	.....
Halteria grandinella	x	x	.....	.....	.....
Gonostomum affine	.....	x	x	.....	.....
Oxytricha setigera	.....	x	.....	.....	.....
Oxytricha pellionella	x	x	.....	.....	.....
Holosticha sp.	x	x**	x	.....	.....

The asterisks indicate the abundance of individuals of a species.
*abundant **very abundant ***extremely abundant

No protozoa grew or lived in the peptone cultures. Fifteen species were recorded from both the soil and peat extract media, seven species from the yeast extract medium with two species of *Colpoda* very abundant, and only three species of ciliates lived in the yeast extract-peptone-glucose medium and only one species, *Colpoda steinii,* multiplied, the other two dying out. *C. steinii,* however, in this last medium attained very great numbers.

These results are in agreement with those of Dixon. Soil extract and peat extract, which are nearest the natural habitat of the fauna, supported the greatest number of species, although not always the greatest number of individuals. Yeast extract and yeast extract-peptone-glucose, typical enriched media, permitted the growth of only a limited fauna, but particular species showed greatly increased growth rate in these media and this is particularly noticeable for *Colpoda inflata* and *C. steinii* in the first and *C. steinii* in the second. It is to be noted that *C. cucullus* did not show any marked increase of growth in the first enriched medium and did not survive at all in the second. This species, in distinction to the other two species, has proved much more difficult to maintain in serial sub-culture using yeast extract, although it grows well in hay extract, soil extract or peat extract. In yeast extract, if kept in permanent culture, not only is the division rate depressed but abnormality of shape and size often occur. The effect of the enriched media, in distinction to the "natural" media, is to select certain species of the original fauna and favour their growth and multiplication while inhibiting the growth and multiplication of other species.

Growth at different depths

It has been found that, with laboratory cultures, certain species are found only, or chiefly, at the surface of the culture, while others are found only, or chiefly, at the bottom. Some from both top and bottom are found in the intervening space (Woodruff 1912).

Peat extract medium was placed in three 4" x 1" tubes to a depth of three inches. The tubes were inoculated with protozoa from the beech culture previously used. Surface and bottom samples were pipetted off at regular intervals and the protozoan fauna recorded. The results are given in Table II. The chief distinction between the two faunas is the presence of the rhizopods at the bottom and their absence, except for one species, from the surface. This may be attributed to their amoeboid habit and their concentration on a solid substrate. Of the ciliates, eleven species are common to both faunas, one species was found only at the surface, and seven only at the bottom. The segregation of seven species to the bottom of the culture may be attributed partly to their habit of creeping over surfaces (Picken 1937), or, in the case of *Vorticella,* to their attachment to the substrate. It may partly be attributed to the debris at the bottom of the tube which afforded a source of food. There is also the possibility that the segregation of the two faunas is due to the carbon dioxide concentration, which would be higher at the bottom than at the surface (Fauré-Fremiet 1950).

Growth at different pH

Ecological surveys, such as those of Wang (1928), have suggested that pH limits the distribution of certain species. Darby (1929) has attributed the greatest significance to changes in pH in explaining the protozoan sequence of ponds. Cutler and Crump (1935), using glucose filters, found that certain species, viz. *Cinetochilum margaritaceum,* did not occur below pH 5.7, and others, viz. *Pleuronema chrysalis,* increased in numbers above pH 6.0. *Colpidium colpoda* and *Paramecium putrinum* also reached their maxima between 6.0 and 7.0, whereas *Arcella vulgaris* preferred a strongly acid reaction below pH 6.0. Other evidence on the effect of pH comes from pure cultures. These generally show that most common fresh water species will grow over a relatively wide range of pH, but that they have an optimum range and often distinct maxima separated by considerable pH differences (Kudo 1946; Loefer 1938). Some species have a very restricted range (Jenkin 1927; Saunders 1924). Watson (1944) working with *Balantiophorus minutus,* a coprophilic species, found that it had a range from 4.65 to 9.25 with maxima at 7.0 and 8.7 and minima at 5.0 and 8.0, which Watson attributed to the increased viscosity of the mucus at these values. Hoare (1927) found that the pH range of three other coprophilic species was very similar. Nasir, quoted by Sandon and Cutler and Crump, found the pH range of *C. cucullus* to be 3.5 to 9.75 and Morea (quoted by Kudo) found that the same species had a range 5.5 to 9.5 with maxima at 6.5 and 7.5. Collett (1919, 1921) showed that it was not only the pH but also the type of ion, particularly the type of anion, which is important in determining the relative toxicity of an acid solution to ciliates.

TABLE II. Vertical distribution of protozoan species in test tube cultures

Protozoan Species	Surface	Bottom
RHIZOPODA		
Biomyxa vagans	..	x
Mayorella vespertilio	..	x
Trichamoeba sp.	x	x
Raphidiophrys elegans	..	x
Trinema lineare	..	x
Euglypha denticulata	..	x
Pontigulasia compressa	..	x
Difflugia arcula	..	x
CILIATA		
Enchelys sp.	..	x
Plagiopyla sp.	..	x
Trichopelma sphagnetorum	x	x
Frontonia depressa	x	x
Colpoda cucullus	x	x
Colpoda inflata	x	x
Colpoda steinii	..	x
Cyrtolophosis mucicola	x	x
Cyclidium glaucoma	x	x
Bryometopus pseudochilodon	x	x
Blepharisma steinii	x	..
Phacodinium metschnicoffi	x	x
Halteria grandinella	x	x
Oxytricha setigera	..	x
Oxytricha pellionella	x	x
Onychodromus grandis	..	x
Holosticha sp.	x	x
Gonostomum affine	..	x
Vorticella striata	..	x

Culture media of known salt concentration were prepared, using NaCl, 0.4g, KCl, 0.016g; $CaCl_2$, 0.024g; distilled water, 4 litres. The media were buffered with 0.2% KH_2PO_4 and the pH adjusted with KOH and HCl to 4.4, 5.2, 6.4, and 7.4. Nonnutrient agar in Syracuse watch glasses was used as a base for these cultures and inoculations of bacteria (*Pseudomonas* sp.) from glucose-peptone slopes provided food. The cultures were inoculated with ciliates from the same beech litter culture, which was strongly acid (pH 4.0). From these cultures further sub-cultures were prepared using the salt and phosphate media adjusted to pH 4.4 in equal proportion with peat extract.

Table III shows the growth of the different species in the initial sub-cultures. Although more species grew in the culture nearest in pH to the original beech culture, most of the species also grew at pH 6.4. At pH 7.4 the five species present were those most common in the beech culture and most widespread in soil and litter. In the further sub-cultures at pH 4.4, *Phacodinium metschnicoffi, Bryometopus pseudochilodon, Blepharisma steinii* and *Holosticha* sp. all grew well. In the case of *Bryometopus* this was particularly interesting as it was not recorded in the original sub-culture.

TABLE III. Growth of protozoa in sub-cultures of different pH

Protozoan species	4.4	5.2	6.4	7.4
RHIZOPODA				
Biomyxa vagans	x	x	x	. .
Mayorella vespertilio	x	x	x	. .
CILIATA				
Trichopelma sphagnetorum	x	x	x	x
Colpoda cucullus	x	x	x	x
Colpoda inflata	x	. .	. .	x
Colpoda steinii	x	x	. .	x
Colpidium sp.	x	x	x	. .
Cyrtolophosis mucicola	x	. .	. .	. .
Blepharisma steinii	x	. .	. .	. .
Phacodinium metschnicoffi	x	. .	x	. .
Oxytricha setigera	. .	. .	x	. .
Oxytricha pellionella	x	. .	. .	. .
Holosticha sp.	x	. .	x	x

RELATION BETWEEN BACTERIA AND CILIATE GROWTH

Introductory

Many free-living ciliates are bacteria feeders. The nature of the bacterial flora is therefore of great importance in their ecology. Two important factors are the edibility of the bacteria and the ciliates' power of selection. Work on these problems up to 1932 is reviewed by Sandon (1932). There is also much information in Kahl (1930-1935). Only the more recent work will therefore be reviewed here.

Leslie (1940) working with *Paramecium* and using carefully standardised conditions found that not only the strain of bacterium but also the age of the bacterial inoculum was important. He found that with suspensions of some bacteria *Paramecium* maintained a high fission rate over a long period, with other bacteria a low fission rate, while some cause the premature death of the ciliate. Leslie found, as did Hetherington (1933), that different strains varied as much as different species in suitability. He also found the initial concentration of the bacteria to be important, and that too little or too great a concentration were unfavourable to ciliate growth. Bragg (1936) examined the selection of food by *Paramecium trichium.*

Burbanck (1942, 1946) worked with *Colpidium colpoda.* He obtained growth on twenty-seven out of thirty-one strains of bacteria tested. He found the Gram-negative Enterobacteriaciae to support the highest division rates and the Bacillaceae the lowest. An important point noted by Burbanck was that the division rate of the ciliate grown on a particular bacterial strain was determined partly by the culture medium in which it had previously been kept. Hetherington (1933), whose findings are similar to those of Leslie and Burbanck, found that the fission rate differed with the same bacterial strain grown in broth and suspended in salt solution.

Kidder and Stuart (1939a, b) found that with *Colpoda steinii* different bacterial strains gave significantly different fission rates. Their results were similar to those of Burbanck except that they did not obtain good growth with *Pseudomonas.* This bacterium gave good growth with Taylor and Strickland (1938) and it seems possible that Kidder and Stuart were not using an aged culture which Leslie had shown to be important. The results of Singh (1941) generally confirm those of Kidder and Stuart and Singh made the interesting observation that the ciliates differed from the amoebae in their bacterial preference.

Chromagenic bacteria had been found by Chatton and Chatton (1927a, b) to be unsuitable as food for ciliates and to cause cytolysis in *Glaucoma scintillans, Colpidium colpoda, Colpoda cucullus, C. steinii, Paramecium caudatum* and *Glaucoma* (syn. *Tetrahymena*) *pyriformis.* Kidder and Stuart confirmed that pigmented strains of both *Pseudomonas* and *Serratia* were toxic to both active and encysted *Colpoda.* They showed that this toxicity was entirely due to the pigment which diffused through the cyst membrane. They found that *Colpoda* could become adapted to *Serratia* but not *Pseudomonas.* Earlier Philpott (1928) had shown that *Paramecium* could become adapted to one strain of toxic bacteria, *B. pyocyaneus,* but not to another, *B. enteritidis.*

Hetherington found that *Gaucoma scintillans* and *Tetrahymena pyriformis* grew well on *E. coli* but poorly on *B. subtilis,* whereas *E. coli* was toxic to *C. colpoda* which grew well on *B. subtilis.* Both *E. coli* and *Ps. fluorescens* and their metabolites were toxic to *Stentor coeruleus*. Chatton and Chatton (1925a, b, c) found that a certain strain of *E. coli* caused abnormalities in *Colpidium campylum*. These included chain formation. Sonneborn (1932) recorded the same effects with *Micrococcus* and *Colpidium campylum*. Chatton and Chatton also found that the different bacterial strains affected conjugation in *Glaucoma* and *Colpidium* and that the latter was particularly affected by *E. coli*.

In a culture of mixed bacteria the ciliates will select only the edible strains and leave the inedible strains which will consequently increase in numbers. This was found to be the case by Kidder and Stuart (1939a). It also explains why Phillips (1922) found that mixed bacterial strains gave better results than single strains for there is a better chance of edible strains being present in a mixed culture. If an edible strain is supplied however, best growth is obtained with just a single strain (Leslie 1940). Singh (1941) found that in the presence of an inedible strain *Colpoda* encysted as it would have done in a non-nutrient medium.

Protozoa may effect a marked and rapid reduction of bacterial numbers. Hoffman (1905) and Huntermuller (1905) reported protozoa feeding on typhoid bacteria. In activited sludge, and other places where bacterial digestion is taking place, they assist by constantly feeding on the bactera and so maintaining a young and vigorous bacterial culture, by aerating and mixing the suspension by the constant beat of their cilia, and by flocculating the particles, partly by the secretion of mucus (Barker 1946; Watson 1946). An important role attributed to bacteria by Purdy and Butterfield (1918) and Butterfield (1929) is the concentration into bulk of dissolved substances. The same function can be attributed to the bacteria-feeding protozoa and this intermediate role in the food chain is stressed by Bond (1933) and Lucus (1947).

Not only do the protozoa select the bacteria, the bacterial flora also has a selective effect on the protozoan fauna (Crozier 1923). Since ciliate species differ not only in their tolerance of different bacterial strains but also in tolerance or different stages of bacterial decomposition the fauna will change with the flora. This has been demonstrated by Hetherington (1933) in the laboratory and observed in nature by Gray (1951, 1952). Further evidence is given in this paper. The sensitivity of certain ciliate species to enriched culture conditions is identical with their sensitivity to bacterial activity. The species may therefore be considered sensitive to the specific bacteria involved or they may be considered sensitive to the concomitant conditions of bacterial activity, viz. increased acidity, lowered oxygen tensions, and increased carbon dioxide tensions. The increased acidity is itself primarily connected with carbon dioxide production so that the chief factor determining the survival and growth of ciliates in an enriched or bacterial culture is their tolerance to carbon dioxide.

Experimental

A sample taken from a drain overhung by willows and with little or no photosynthetic flora was found to contain principally two ciliates, viz. *Paramecium caudatum* and *Euplotes aediculatus*. *Vorticella striata* and *Lembadion bullinum* occurred in small numbers but no other ciliate species were observed. Some of the material was pipetted into Syracuse watch glasses and loops of bacteria (*Proteus* sp.) added.

After twenty-four hours there was little change in the fauna although the *Euplotes* were unhealthy and fewer in number. After forty-eight hours the *Paramecium* were present in very great numbers, massed together and dividing rapidly. *Chilodonella dentata*, *Cyclidium glaucoma* and *Oxytricha pellionella* were also present in large numbers. *Euplotes* and *Lembadion bullinum* had died out completely. *Vorticella striata*, though still present, showed no change in numbers although the individuals had increased in size. After ninety-six hours the culture, previously turbid with bacteria, had cleared. There were many dead but no living *Paramecium*. *Chilodonella* and *Cyclidium* had disappeared. *Oxytricha* was still present in large numbers and a few *V. striata* were dividing. Algae, both green and yellow brown, were increasing in numbers. Subsequently the ciliates disappeared entirely from the culture which was filled with algae.

The fauna of the present sample is similar in some respects to the fauna of the oxidation pond described in another paper (Stout 1954a) and is composed largely of meso- and polysaprobic species. *Paramecium caudatum* is most common in waters subject to pollution (Lackey 1938) and occurs in large numbers only in polluted water or sewers (Green 1925; Hassall 1850, 1855). The same is largely true of *Chilodonella dentata*, *Cyclidium glaucoma* and *Oxytricha pellionella* (Lackey 1938), but *Euplotes aediculatus*, *Vorticella striata* and *Lembadion bullinum* are not so recorded (Noland 1925).

The most interesting record of *Paramecium* under natural conditions is that of Gray (1951, 1952) who found *P. caudatum* and other species present in very large numbers in a polluted stream and occurring whenever the stream became turbid after rains and organic and faecal matter were washed into it. When these conditions disappeared *Paramecium* disappeared also. This is the condition simulated by the present culture: the death of the non-pollution species (*Euplotes* and *Lembadion*), the growth of pollution species (*Cyclidium, Oxytricha, Chilodonella* and *Paramecium*), and the disappearance of the ciliates when the culture clears. Under natural conditions it is very probable that *Paramecium* would survive in small numbers at the bottom of the stream, where conditions are closer to its favoured habitat, and not die as in the present experiments. Normally the end of a hay infusion culture is marked by the presence of the ciliates at the bottom of the culture (Jones 1930), and Green found them in greatest numbers at the bottom of the sewer. Lindeman (1942) and Lauterborn (1916), amongst others, have recorded *P. caudatum* from bottom, though not mud, samples and Lindeman has shown that they survive for a long period even under anaerobic conditions if the temperature is low.

The ecological significance of the present experiment is in the selective effect of the bacteria upon the ciliate fauna and in the apparent dependence of certain species upon the presence of bacteria. There is a marked difference between those species which become moribund and die when bacteria are present in large numbers and those species which multiply very rapidly in bacterial infusions. Noland (1925) observed that the species developing in laboratory infusions were quite distinct from species found in the field and were, indeed, rare in fresh water. An interesting contrast between two species of the same genus is shown by the reactions of *Vorticella striata* and of *V. microstoma* to high bacterial concentrations. *V. striata* survives but does not grow or divide to any extent. Under similar conditions *V. microstoma* increases greatly in size to become *V. hians*, an infusion form first described by O. F. Muller (1773), and divides very rapidly, like *P. caudatum*. Like *P. caudatum* this growth continues while the bacteria are present but upon the disappearance of the bacteria *V. microstoma* encysts (Brand 1923; Stout 1954a). This is the chief distinction between two species which are morphologically very similar (Noland and Finley 1931. Crozier (1923) formulated a generalization that the abundance of ciliates in any habitat, and particularly sewage filters was inversely proportional to the diversity of species but this generalization, while it emphasizes the selective effect of polluted waters, is not always correct. In the present experiment, for example, there were more species as well as more individuals following the inoculation of bacteria.

Reaction to Carbon Dioxide

Introductory

The most comprehensive account of the effect of pure carbon dioxide on ciliate protozoa is that given by Jacobs (1912) in a paper that has been generally overlooked. Jacobs also published a number of papers on carbon dioxide narcosis, the most important of which is that of 1922. Watson (1944) studied the effect of pure carbon dioxide on two ciliates, *Balantiophorus minutus* and *Paramecium caudatum*. Root (1930) and Pace and Ireland (1945) studied the effect of carbon dioxide tension on *Paramecium caudatum* and *Tetrahymena pyriformis* respectively.

The response of the ciliates to high carbon dioxide tensions is at first negative. They migrate away from high concentrations, although low concentrations may attract certain species (Jennings 1915). As narcosis takes place the ciliates swim more and more slowly and the body becomes rounded. They cease to move, though the cilia may still beat freely. At this stage recovery may be obtained. Finally there is no further activity and the ciliates blister. This description, drawn from the reactions of *Paramecium* fits most ciliates. Those that are very sensitive succumb immediately while those that are very resistant will continue to swim slowly, but not feed, for many hours. In *Vorticella* the peristomial cilia cease to beat almost immediately.

The effect of carbon dioxide is first stimulatory, marked by acceleration of swimming, and then depressive. The cytoplasm first liquefies and then coagulates. As coagulation of the cytoplasm is the prelude to death it occurs earlier in the sensitive species and later in the more resistant species. Oxygen consumption is first stimulated and then depressed (Root 1930). Chang and Loomis (1946) after discussing carbon dioxide narcosis conclude that it results from rapid penetration, increases in cellular activity and the formation of specific but weakly bonded protein compounds.

Jacobs (1912) found that several factors, including temperature, affected his experimental results. He also found that there was great variation in the different experiments and that different clones and different cultural conditions affected the results. The period of survival varied between almost instantaneous death (*Coleps hirtus*) to prolonged survival (*Colpidium colpoda*). To some extent ciliates can be acclimatized to increased carbon dioxide tensions.

While the present experiments generally confirm Jacobs' results there is one important difference, viz. *Colpidium colpoda,* which was found in the present experiments to be relatively sensitive whereas it was the most resistant species recorded by Jacobs. Hetherington (1933) points out that *Colpidium colpoda* is comparatively rare and that until the publication of a paper by Bresslau (1922) *C. campylum* was frequently called *C. colpoda.* Hetherington found that *C. colpoda* did not tolerate extremely acid conditions and was not found in laboratory infusions at the most intense period of bacterial degradation. I am inclined to think, therefore, that Jacobs' *Colpidium* was probably *C. campylum* and not *C. colpoda.*

Experimental

The technique was similar to that used by Watson (1944). Carbon dioxide was passed through a chamber in which hanging drops containing the ciliates were suspended (Stout 1954b).

The maximum survival time of the ciliates tested both in an atmosphere of pure carbon dioxide and in a 1:1 mixture of carbon dioxide and oxygen is given in Table IV. The ciliates fall into four groups. First, sensitive species, including *Stylonychia, Stentor, Vorticella campanula, Lembadion bullinum, Coleps* and *Euplotes aediculatus.* These succumbed very rapidy to the carbon dioxide even when mixed with oxygen. *Stentor* reacted first by becoming detached from its base. Secondly, moderately sensitive species, viz. *Glaucoma, Colpidium, Cinetochilum, Cyclidium, Paramecium bursaria* and *Podophyra.* These ciliates did not survive more than quarter of an hour in the pure carbon dioxide atmosphere. Thirdly, the resistant species which survived over a quarter of an hour in pure carbon dioxide. These include *Lacrymaria, Lionotus, Paramecium caudatum, Euplotes patella, Aspidisca costata* and *V. striata.* Fourthly, the very resistant species which survived for several hours including *Trichopelma, Colpoda steinii* and *C. inflata. Vorticella microstoma* formed a telotroch which survived many hours (Stout 1954b). *C. steinii,* the most resistant of the ciliates tested survived twenty-four hours in an oxygen-carbon dioxide atmosphere moving slowly but not feeding or dividing (Stout 1955).

REACTION TO ANOXIA

Introductory

TABLE IV. Survival of ciliates at high carbon dioxide tensions

Fresh water species	Survival Time (Minutes)		Comment
	CO$_2$	O$_2$/CO$_2$	
Coleps hirtus	....	<10	
Lacrymaria olor	>15	....	
Lionotus fasciola	>30	..	
Paramecium bursaria	<15	<25	
Paramecium caudatum	>30	....	
Lembadion bullinum	<15	<10	
Glaucoma scintillans	<15	<15	
Colpidium colpoda	<15	.	
Cinetochilum margaritaceum	<15	....	
Cyclidium glaucoma	<15	<15	
Halteria grandinella	....	<25	
Stentor sp.	<15	....	Detached from its base after 10 minutes.
Stylonychia mytilus	<15	<10	
Euplotes patella	>15	..	
Euplotes aediculatus	<15	.	
Aspidisca costata	>30		
Vorticella campanula	<15		
Vorticella convallaria	>15	..	
Vorticella striata	>15		
Vorticella nebulifera	>14	...	
Podophrya fixa	<15	....	

Soil and sewage species	Survival Time CO$_2$	Comment
Trichopelma sphagnetorum	3 hours	
Colpoda cucullus	<15 minutes	
Colpoda inflata	2 hours 30 minutes	
Colpoda steinii	2 hours 50 minutes	Old culture
	6 hours	Fresh culture
	(O$_2$/CO$_2$) 24 hours	No feeding or division
Vorticella microstoma	20 hours (telotroch	Telotroch formation

The experimental evidence of anaerobiosis falls into two groups: that which involves the bubbling of gases through the culture (Nikitinsky and Mudrezowa-Wyss 1930), and that which involves the removal of oxygen either by use of a bell jar or by a small chamber in which a hanging drop is suspended. It was this last method that was used in the present tests. Previous work with this apparatus or with a manometer under much the same conditions has given very diverse results even when the same species is being tested. There are three different reactions described: first, the immediate blistering of the ciliate (Gersch 1937; Specht 1934); secondly, the survival of the ciliate for a short period followed by blistering (Kitching 1939a, b; Johnston and Evans 1941a; Adolph 1929); thirdly, the survival of the ciliate indefinitely (Thomas 1942; Watson 1944).

A comprehensive review of anaerobiosis in ciliates is given by Thomas (1942) and Brand (1946). Not only is there some conflict between the experimental results obtained with the same species by different workers but often there is also a marked discrepancy between the experimental and ecological evidence. Typical of the conflicting results are the tests with *Paramecium caudatum.* Putter (1905) recorded survival of this ciliate at room temperatures for ten days, Nikitinsky and Mudrezowa-Wyss (1930) also at room temperatures recorded survival for eighteen days, Gersch (1937) recorded death at room temperatures in ten seconds, Barbarine (1938) recorded survival of starved ciliates for an hour and fed ciliates for more than two days, Kitching (1939b) recorded maximum survival of twelve hours at 24°C to 28°C, Liebmann (1936) recorded survival for three days at room temperature and Lindeman (1942) recorded survival for less than thirty days at 10°C but more than thirty days at 0°C and 5°C Watson (1944) recorded that *P. caudatum* survived less than two hours at room temperatures although *Balantiophorus minutus* survived indefinitely under the same conditions. In evaluating these results the experiments of Kitching and Watson, which both assured the complete absence of oxygen, may be taken as a general guide. It may be concluded then that *P. caudatum* is a facultative anaerobe but that it can survive only a limited period in the complete absence of oxygen. Well fed ciliates survive better than starved ones and the ciliates survive longer at lower temperatures than high (Fauré-Fremiet 1929a, b).

Nearly all the experiments that have been recorded have been done with impure cultures. An exception is the work done on axenic cultures of *Tetrahymena pyriformis* by Thomas (1942) and Pace and Ireland (1945). Thomas, who studied the anaerobic carbohydrate metabolism of the ciliate, reported that the ciliates under anaerobic conditions were sluggish, moved slowly and did not divide. Some of his experiments lasted fifty-two hours without the death of any of the ciliates. Pace and Ireland, using an apparatus which involved partial evacuation of the experimental chamber and subsequent replacement with gas of known constitution, recorded death of the ciliates in one experiment and growth in another. Obviously their technique was unsatisfactory and there seems no reason to doubt that *Tetrahymena pyriformis* is a true facultative anaerobe. Another indisputable case of facultative anaerobiosis in a free-living ciliate is that of *Balantiophorus minutus* which, like *T. pyriformis,* moves sluggishly but does not divide, although in Watson's experiments it survived for over twenty days. *Metopus es* is an obligate anaerobe and can both divide (Lackey 1938) and conjugate (Noland 1927) in the complete absence of oxygen. Three groups of ciliates then can be distinguished. First, the obligate aerobes which die immediately on the removal of oxygen. Second, the facultative anaerobes which consist of those species able to survive more or less indefinitely, e.g. *Balantiophorus minutus* and *Tetrahymena pyriformis,* and of those species which can survive for only a limited period, e.g. *Paramecium caudatum.* These species cannot divide in the absence of oxygen. Third, the obligate anaerobes which cannot be successfully cultured at high oxygen tensions but which grow well in the complete absence of oxygen, e.g. *Metopus es.* A careful review of the literature shows that there is not such a great discrepancy between the experimental and ecological evidence as at first appears. In many cases faulty technique invalidates the experimental work and in other cases low temperatures account for a survival period longer than that recorded by other workers.

Experimental

A modification of Kitching's apparatus was used. Nitrogen was used to replace the oxygen in the chamber and maintain an oxygen-free atmosphere. Some difficulty was experienced both in maintaining the chamber in an oxygen-free state and in securing reproducible results. It was found that if the ciliates were transferred to the chamber immediately after preparation of the hanging drop and the oxygen removed death would occur, whereas if the drop was left for a little while (say overnight) better survival could be obtained. Also slow replacement of the oxygen secured better survival than rapid replacement. Nevertheless the results indicated that facultative anaerobiosis under the conditions of the experiment was limited to only some ciliates, whereas many typical fresh water species survived only a very short time after the removal of the oxygen, although recovery could be obtained if oxygen were reintroduced. Occasionally photosynthetic organisms were present in the hanging drop preparations and *Paramecium bursaria* has a photosynthetic symbiont. In these cases a trace of oxygen may have been evolved by photosynthetic activity. The results are summarised in Table V.

The ciliates tested fell into two groups: first, those that blistered within a few hours, viz. *Stylonychia mytilus, Halteria grandinella, Vorticella campanula* and *V. canvallaria;* and second, those that generally survived for many hours, e.g. *Coleps hirtus, Cyclidium glaucoma* and *Cinetochilum margaritaceum.*

Vorticella campanula and *V. convallaria,* although they blistered very quickly, first reacted by detaching themselves from their stalks. Due to the rapidity with which they blistered, however, normal telotroch formation was interrupted by by death. In the case of *V. microstoma* there is normal telotroch formation and the telotroch survives for many hours. (Stout 1954b.) The re-

TABLE V. Survival of ciliates at low oxygen tensions

Fresh water species	Survival Time (Hours)	Comment
Coleps hirtus	124	No observed adverse effects
Lionotus sp.	48	"
Lionotus fasciola	24	"
Chilodonella sp.	48	"
Paramecium bursaria	124	"
Paramecium aurelia	76	Variable results
Paramecium caudatum	72	"
Paramecium caudatum	113	With *Chlorella*
Glaucoma scintillans	20	
Cinetochilum margaritaceum	76	Variable results
Cyclidium glaucoma	124	"
Stentor roeseli	24	Became detached and free-swimming
Halteria grandinella	24	Usually narcotized within an hour
Oxytricha pellionella	113	With *Chlorella*
Stylonychia mytilus	1	Is narcotized very rapidly
Euplotes patella	48	
Euplotes aediculatus	22	Few ciliates tested
Vorticella campanula	2	Both vorticellid species form telotrochs, detach from their stalks and are soon narcotized
Vorticella convallaria	2	

Soil and sewage species	Survival Time (Days)	Comment
Trichopelma sphagnetorum	24	
Colpoda steinii	7	Encysts on exhaustion of food
Colpoda inflata	3	"
Colpoda cucullus	3	"
Cyclidium glaucoma	1	Did not survive with *Trichopelma*
Metopus sp.	7	No observed adverse effects
Vorticella microstoma	2 (telotroch)	Forms a telotroch

action of *Stentor,* another sessile ciliate, is in many ways similar. *Stentor roeseli,* the species studied, lives within a gelatinous tube attached at its base to the substrate. The ciliate reacts to lack of oxygen by detaching itself from its base and from its gelatinous tube and swimming freely in the drop. Locomotion is achieved by the same ciliary action which normally causes a current of particles to stream towards the peristome. While swimming *Stentor* rotates slightly on its long axis. The period of survival of the free swimming form is perhaps limited partly by the inhibition of feeding, as, in the present experiments, the individual which became detached twenty-four hours later did not blister.

The reactions of *Colpoda* are dealt with in greater detail elsewhere (Stout 1955). It is sufficient to notice that they are typical facultative anaerobes, that they move sluggishly, feed and ultimately encyst in the absence of oxygen but that they do not divide or excyst. In the same way *Vorticella microstoma,* which survives as a telotroch, does not settle or feed in the absence of oxygen (Stout 1954b).

In experiments with *Metopus* the ciliate survived for a week in the absence of oxygen but did not divide perhaps due to inadequate food. It is not certain whether *Metopus* is a scavenger or whether it feeds on bacteria (Sandon 1932). In the present experiments it was fed on *Proteus* sp.

DISCUSSION

When a mixed sample of fresh water ciliates is transferred to an enriched culture the species which develop differ from the common fresh water species and are chiefly those which are found just above the mud level near the bottom of lakes or streams or in polluted water (Noland 1925). This fauna is largely bacteriophagous with a few carnivorous species, e.g. *Dileptus,* feeding on the bacteriophagous species. In contradistinction, the ordinary fresh water fauna is either carnivorous, e.g. *Stentor,* or herbivorous, i.e. feeding on diatoms or plankton and flagellates (Picken 1930; Gray 1951, 1952). Noland's interpretation is that the fauna in each case is determined by its food requirements, a thesis also supported by Picken and Gray, and for this reason the diatom-feeders are associated with the diatom flora and the bacteriophagous species with bacterial infusion. However, most species have a comparatively wide food range (Sandon 1932), and the exclusion of most fresh water species from bacterial infusions is due not only to the absence of suitable food but also to the adverse conditions which develop. That this is so is amply borne out by the present experiments which give some clue to the adverse conditions which operate in inhibiting the activity or causing the death of different species.

It has been shown that the species in any particular sample grow best in a culture medium nearest in composition to their natural habitat. If transferred to an enriched medium many species fail to grow or die, although certain species may flourish in enriched conditions. It is presumed that the death of the sensitive species is due to the bacterial activity in enriched media for the same effects can be obtained by adding loops of bacteria to a mixed culture of ciliates. Moreover, it is presumed that the toxicity of the bacteria is due not so much to the cells themselves but to their metabolic activity. This results in the exhaustion of oxygen and the production of carbon dioxide and other gases, such as ammonia and hydrogen sulphide, which are inimical to many species. Moreover, although bacterial infusion is generally accompanied by increased acidity which appears to be harmful to many species, this toxicity is attributed to the increase in carbon dioxide concentration which is reflected in increased acidity. This is thought to be the case because most species have a wide pH range and those species, such as *Cinetochilum margaritaceum* (Cutler and Crump 1935), which have not been found in acid infusions have here been found to be sensitive to high carbon dioxide concentrations, whereas species such as *Paramecium caudatum* which are found in acid infusions, are also found to be resistant to high carbon dioxide concentrations. Similarly *Coleps hirtus* which is less tolerant of strongly acid conditions than *Halteria grandinella* (Lackey 1938) is significantly more sensitive to carbon dioxide.

In the present experiments the three species which survived the richest infusions were *Trichopelma sphagnetorum, Colpoda inflata,* and *Colpoda steinii*. Only the last species grew well in the richest culture. *Colpoda cucullus* which is known to have similar food requirements to the other two species failed to grow in the enriched media and subsequently proved highly sensitive to carbon dioxide. Similarly, in the bacterial experiment, *Lembadion bullinum* and *Euplotes aediculatus* both became moribund and died. Both these species proved very sensitive to carbon dioxide whereas *Vorticella striata* which survived in the bacterial culture is relatively resistant. It is not unreasonable then to conclude that an important factor affecting the protozoan fauna is the carbon dioxide concentration, associated as it generally is with increased acidity. It is this factor, rather than lack of oxygen, which appears to be of greatest significance as a selective ecological factor.

This conclusion is supported when the experimental and ecological evidence is compared. Jacobs' results show that four ciliates survive more than half an hour on the average and four less than half an hour, one dying within a few minutes (*Coleps hirtus*). The more resistant species are all recorded by Noland (1925) from samples rich in carbon dioxide and poor in oxygen and from laboratory cultures. None of the other four species are so recorded. The four resistant species are therefore typical polysaprobes and the others mesosaprobes or oligosaprobes.

Often a species which is resistant to high carbon dioxide concentrations also survives lack of oxygen, e.g. *Colpoda steinii* and *Balantiophorus minutus,* and conversely a species sensitive to high carbon dioxide concentrations is also sensitive to oxygen lack, e.g. *Stylonchia mytilus*. However, in some cases a species is highly sensitive to carbon dioxide but tolerant of anoxia, e.g. *Coleps hirtus,* or, conversely, is relatively resistant to carbon dioxide but is sensitive to anoxia, e.g. *Halteria grandinella*. It is interesting to find that Noland recorded the lowest oxygen saturation for *Halteria* as 16.9% and for *Coleps* 31.7% and the highest carbon dioxide concentration as 14.7 cc/litre (av. 3.7 cc/l.) and 10.7 cc/litre (av. 1.5 cc/l/) respectively. Thus the carbon dioxide sensitivity is generally a better indication of the ecology of a species than anoxia sensitivity and this can also be seen from Noland's figures for the different species of *Vorticella*. Generally in nature strictly anaerobic conditions are rare or of brief duration and gradual change in conditions permits adaptation of the species. But the occurrence of such anaerobic conditions does cause the death of sensitive species just as the presence of high oxygen concentrations excludes obligate anaerobes. This is shown clearly by the data in Table VI, taken from Noland.

TABLE VI. Distribution of ciliates in relation to oxygen saturation (from Noland)

Species	Oxygen saturation %	
	Range	Average
Metopus es	5.3 to 31.7	15.2
Halteria grandinella	16.9 to 173.6	79.7
Stylonychia mytilus	22.7 to 169.2	70.6
Cinetochilum margaritaceum	0.0 to 124.9	66.9
Cyclidium glaucoma	0.0 to 169.2	66.0

These data agree well with the present experimental evidence and show quite clearly that the presence or absence of a species in any particular habitat is determined by some specific physiological character, perhaps sensitivity to, or tolerance of, carbon dioxide or oxygen lack. Food is not the sole, and not necessarily the most important, of these physiological characters. In the case of *Colpoda,* for example, the food requirements of the different species are very similar but one species may be excluded from a habitat in which another may thrive. Similarly, in the above table (Table VI) both *Halteria grandinella* and *Cyclidium glaucoma* are bacteriophagous but one species is excluded from certain habitats because it is not tolerant of anoxia. There is no strict correlation between the different physiological characters. Amongst bacteriophagous species some are more tolerant of carbon dioxide than others, some are facultative anaerobes, others are not. Similarly, both *Metopus es* and *Coleps hirtus* are scavengers, but one is an obligate anaerobe and the other is extremely sensitive to carbon dioxide. *Dileptus,* although a carnivore, is apparently a facultative anaerobe. Within the same genus there may also be considerable differences, e.g. *Vorticella,* with *V. campanula* highly sensitive to anoxia and carbon dioxide and *V. microstoma* very resistant. *Paramecium,* a genus of typically bacteriophagous species, includes the relatively sensitive *P. bursaria* and the polysaprobe *P. caudatum,* which is, interestingly enough, more resistant to carbon dioxide toxaemia than to anoxia.

The reaction of the sessile species, *Stentor* and *Vorticella,* is particularly instructive. In response both to raised carbon dioxide and lowered oxygen tensions these ciliates become detached and free swimming. They settle again when normal conditions are secured. This explains their distribution in nature. Sprugel (1951) found that *S. coeruleus* occurred only within a limited range of pH, carbon dioxide concentration, temperature and oxygen tension. This distribution is accounted for not only by the fact that the ciliates thrive only within a certain range of environmental conditions but also by their reaction to adverse conditions which enables them, by trial and error, to select a favourable environment from one less favourable (Jennings 1915, p. 66). This selection together with the gradual acclimatization of species accounts very largely for their distribution in natural waters. Such selective distribution was found to be the case for *Loxodes rostrum* (Rylov 1923). Conversely Jennings and Moore (1901) found that certain protozoa were attracted by carbon dioxide (including *Paramecium caudatum, Colpidium colpoda* and *Chilomonas paramecium*) while there were indifferent (*Euplotes* and *Euglena*). This is of interest for Pace and Ireland (1945) showed that *Chilomonas paramecium* grew best at a carbon dioxide tension of 100 mm Hg and both *Paramecium caudatum* and *Colpidium colpoda* are found chiefly in association with a rich bacterial flora. Fauré Fremiet (1950) has observed that *Colpidium colpoda* and *C. campylum* are attracted chemotactically by the slightly acid conditions of a *Beggiatoa* colony. It can be seen, therefore, that not only is there a graduation of sensitivity to carbon dioxide but that polysaprobes are actually attracted by acid conditions and it therefore explains why they are rapidly associated with bacterial degradation. The optimum physical conditions are both absolute and relative; absolute in that a certain concentration is invariably toxic, relative in that ciliates can be slowly acclimatized to increased concentrations (Jennings 1915). It is also interesting to note that *Coleps hirtus* is not immediately attracted to the *Beggiatoa* association but appears as a detritus feeder after the destruction of the colony (Fauré-Fremiet 1950).

One most important aspect of their physiology affecting the ecology of ciliates is the formation of cysts. Cyst physiology has been dealt with elsewhere (Stout 1955). It is apparent that it is an important mechanism aiding the survival of species under adverse conditions, particularly desiccation. This will explain why some species, such as *Paramecium caudatum,* which do not encyst but which are otherwise admirably fitted physiologically for, e.g., a coprophilic habit, are not found there, whereas other ciliates of very similar physiology but with a highly developed cyst physiology, are found in this habitat, e.g. *Colpoda.*

Finally mention must be made of the morphology of the species in so far as it affects their ecology. Large species with elaborate feeding mechanisms require an extensive habitat and cannot be confined in capillaries or pore spaces. For this reason soil and coprophilic species are characteristically small, the larger species being excluded because of their size. Picken (1937) treats this relation between morphology, feeding and swimming behaviour and ecology in considerable detail.

In conclusion, then, it can be stated that the ecology of a species is determined in its physiology, its behaviour, and in its morphology. Although this may appear to atomize a study of ciliate ecology, in reality it enables the important features of each species to be defined and contrasted with other species closely related in some way. The selective effect of any habitat on the ciliate fauna can be attributed to the relative significance of the different factors. For example, polluted water rich in organic matter and consequently with great bacterial activity will be inhabited by species that are chiefly bacteriophagous and that are tolerant of high carbon dioxide tensions and perhaps anoxia. If the habitat is subject to recurrent drying then only species with an adequate cyst mechanism will survive. If there is limited water space only the smaller species will be found. Conversely such species as *Paramecium caudatum* or *Tetrahymena pyriformis* or *Balantiophorus minutus* which thrive in such infusions will die out of cultures lacking a rich bacterial flora. In each case it is necessary to consider the positive factors, e.g. food supply, with the negative factors, e.g. high carbon dioxide tensions, before the ecology of any habitat can be defined.

The author is indebted to Prof. L. R. Richardson for helpful criticism during the present studies which form part of a thesis submitted to the University of New Zealand in partial fulfilment of the requirements for the degree of Doctor of Philosophy. During this period the author held a Victoria University College Research Scholarship.

SUMMARY

1. Ciliates are of cosmopolitan distribution but are restricted to certain habitats solely by certain ecological factors. Similar habitats generally have

similar faunas. The presence or absence of different species is determined both by the presence of suitable food and by the selective effect of other environmental factors.

2. Generally ciliates grow best when cultural conditions are closest to those of their natural environment. In enriched cultures, although some species grow well, most die out. Those species which grow well are those most widely distributed in nature.

3. Similarly most species are sensitive to high bacterial concentrations. Those species which thrive in high bacterial concentrations are those species which grow best in enriched media.

4. There is a wide range of sensitivity to high carbon dioxide tensions. Some species are very sensitive, some moderately resistant, and some very resistant. This criterion distinguishes oligosaprobic, mesosaprobic and polysaprobic species. Species tolerant of enriched cultures and tolerant of high bacterial concentrations are resistant to high carbon dioxide tensions. Conversely, species sensitive to enriched cultures and high bacterial concentrations are sensitive to high carbon dioxide tensions. Further, species sensitive to acid conditions are sensitive to high carbon dioxide tensions whereas acid-tolerant species are tolerant of high carbon dioxide tensions. As carbon dioxide is the chief determinant of pH in most natural waters and laboratory cultures, it is concluded that it is the primary adverse factor affecting the distribution of ciliates and the chief factor distinguishing pollution from non-pollution species.

5. Similarly, species differ in their reactions to reduced oxygen tensions. Some are very sensitive, some moderately tolerant and some are facultative anaerobes. There is no obvious correlaton between tolerance of low oxygen tensions and tolerance of high carbon dioxide tensions. Some facultative anaerobes are extremely sensitive to high carbon dioxide tensions, while some polysaprobic species are not facultative anaerobes. In the complete absence of oxygen facultative anaerobes cannot divide, though they will feed and move freely.

6. The bionomics of ciliates are determined by their physiological reactions to environmental factors, by their life history, and by their morphology. Habitats subject to desiccation support only the growth of small species which encyst and excyst regularly. Larger species, with elaborate feeding mechanisms, are confined to habitats with an extensive volume of water.

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NOTES AND COMMENT

NOTES ON A BLOOM OF *EUGLENA HAEMATODES* IN OHIO

Striking blooms of red euglenas have been described a number of times in Europe (*e.g.,* by Baumeister 1954, Ehrenberg 1838, Härdtl 1935, Heidt 1932, Huber-Pestalozzi 1955, Károly 1887, Klausener 1908, Kol 1929, Mainx 1927, Naumann 1915-16, 1925, Schmitt 1947, Szabados 1936), America (Gojdics 1953, Johnson 1939, 1942), and elsewhere (Carter 1869, Ehrenberg 1830, Hardy 1911, Kashyop 1908).

A bloom of *Euglena haematodes* (Ehrenberg) was observed on July 3, 1955 in a neglected, weed- and alga-filled farm pond in Chester Township, Geauga County, Ohio, at which time it was poorly developed except in the inaccessible central portions of the pond. Specimens were collected from peripheral locations and returned to the laboratory for identification. The pond was approximately circular, with a surface area of about 2000 m^2.

A second visit was made to the pond on July 7, at which time a skiff was used in order to make the central portions available. The bloom had greatly increased in extent, so that an area estimated to be 7 m. wide and 40 m. long appeared as though brilliant red paint had been spilled on the water (Gojdics (1953) has described blooms of red euglenas in similar terms). At close range, however, the red patches had a powdery appearance very similar to sporulating rust. It was clear that the individual organisms were not submerged in the water, but constituted a neuston.

The surface of the pond was examined carefully with a dissecting microscope magnifying 18 and 27 times. The undisturbed red patches were seen to consist of a single layer of emergent red cysts, resting like tiny bubbles upon the surface film. Where they were abundant, they touched each other side by side to form adhesive floating mats. Beneath the red cells, not emergent, were lesser numbers of the cysts of another, undetermined species of smaller, green *Euglena,* and also large numbers of the desmid, *Closterium* sp. The latter was the dominant plankter of the underlying water, and apparently only incidentally occurred in the surface film.

Samples of the surface film were obtained by carefully slipping microscope slides beneath red patches, and examing them immediately, without cover slips, under a compound microscope. It was estimated that there were an average of 800 cysts / $mm.^2$ of surface in the patches, or, assuming half the surface in the affected area of the pond to be covered with the mat of cysts, 400,000,000 / $m.^2$ The only previous quantitative estimate of *E. haematodes* (or other red, neuston-forming species of *Euglena*) appears to be those of Naumann (1915-16, 1925), who estimated there were 100-500 cysts / $mm.^2$ in the ponds he studied in southern Sweden.

Blooms of red euglenas have been noted to occur, for the most part, after periods of high temperature (Jahn 1946) and brilliant sunshine (Huber-Pestalozzi 1955), and the bloom described here is no exception. Water temperatures were taken on the second visit. Undisturbed water at a depth of 40 cm. was 25° C., while that in the upper cm. measured 33° C. At the very surface, where the cysts were floating, the temperature undoubtedly was even higher.

Specimens were collected in large numbers in a wide-mouth, 10 liter glass container. In the process the surface mats were immersed, and within half an hour they had sunk to the bottom. Examination at this time showed that the majority of the encysted individuals had become active, though their swimming movements were impeded by a mass of gelatinous material. On the following day, the gelatinous mass had largely disappeared. The specimens were for the most part encysted again, on the bottom.

Generous samples were transferred to finger bowls, and placed in a greenhouse fully illuminated by the sun. The temperature of the water in the finger bowls quickly increased from 27° C to 34° C. The vast majority of the specimens became active, and large numbers of them came to the surface and formed typical floating cysts, such as had been observed at the pond. In control containers the individuals remained, for the most part, inactive on the bottom.

The rest of the individuals remaining in the 10 liter container were very crowded. After another day, with neither any special illumination nor an increase of temperature, large numbers came to the top and encysted. Each encysting individual secreted a gelatinous envelope, within which there was little or no motion. When immersed in water the encysted specimens rotated, then broke from the envelopes, and either swam, performed metabolic movements or both. Three days later most cysts clearly showed two concentric gelatinous layers, and a few had three distinct layers. At the end of 12 days, the specimens which remained on the bottom were mostly dead, or moribund, whereas there was a continuous scum of spongy gelatinous material on the surface of the water fully a mm. thick, in which were embedded myriads of healthy cysts of *E. haematodes.* By far the majority of the specimens were motionless, but in among them were a number of swimming and/or metabolic specimens. No remaining trace of individual cyst walls could be seen in the gelatinous matrix, all the envelopes of the numerous specimens apparently having merged to form a single gelatinous mass. At this time very few of the cysts emerged above the surface as individuals. Härdtl (1935) has described a similar gelatinous mat of *E. heliorubescens* 2-3 mm. thick.

Blooms of *E. haematodes* have not been reported from Ohio, though Gojdics (1953) has reported them from eastern Pennsylvania and Tennessee. Neither Landacre (1908) nor Walton (1915) reported *E. haematodes* from Ohio, but they listed the closely related *E. sanguinea* from Sandusky and Cedar Point, without making it clear that they observed it to bloom. In contrast to Gojdics (1953), Huber-Pestalozzi (1955) has reservations concerning the distinction between *E. sanguinea* and *E. haematodes.* The specimens forming the bloom described above had distinct eyespots, and the spiral surface striae were visible only on an occasional individual, even when viewed with an oil immersion lens. According to Gojdics' keys and descriptions it clearly belongs to the species *E. haematodes.* According to Huber-Pestalozzi, on the other hand, it had the clear eyespot of *E. sanguinea* and the obscure surface of striae of *E. haematodes.*

SUMMARY

Euglena haematodes formed a brilliant red bloom on the surface of a neglected farm pond. The bloom was

examined *in situ* by means of dissecting and compound microscopes. Specimens had formed rafts of cysts resting above the surface film of the water, thus forming a true neuston. There was an average, in the rafts, of 800 cysts / mm.^{2} on the surface. Observations also were made in the laboratory. High temperature and brilliant illumination stimulated the formation of surface cysts, as did crowded conditions. In 12 days, a crowded culture formed a gelatinous surface mat a full mm. thick, within which were encysted myriads of specimens. Blooms of red euglenas have not previously been reported from Ohio.

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GROWTH AND PHENOLOGICAL OBSERVATIONS OF ARIZONA JUNIPERS

To obtain information on the seasonal development of the four tree-sized juniper species found in Arizona, a growth and phenological study[1] was carried on in 1939 and 1940, in a pinyon-juniper woodland near Walnut Canyon, 10 miles southeast of Flagstaff, Arizona, at an elevation of 6,500 feet. The pinyon-juniper woodland in this locality is composed of pinyon (*Pinus edulis* Engelm.), Utah juniper (*Juniperus osteosperma* (Torr.) Little), one-seed juniper (*J. monosperma* (Engelm.) Sarg.), Rocky Mountain juniper (*J. scopulorum* Sarg.), and alligator juniper (*J. deppeana* Steud.). To determine the seasonal leader elongation of the four species of juniper, young vigorous trees were selected for study. A string was tied around the leader 100 mm. from the tip to serve as a reference point and measurements were taken at intervals of 1 to 2 weeks with a steel rule. Leader growth of the four species of juniper for 1939 and 1940 are shown in Figure 1. Rainfall and soil temperature during the two growing seasons were measured near the trees. Soil temperatures were obtained weekly at 10:00 A.M. at a 3-inch depth under pinyon canopy.

There was almost three times as much rain between May 1 and October 31 in 1940 as in 1939. Also the summer rains began earlier in 1940 than in 1939. Coincidently, the average leader growth for the study trees during the 1940 growing season was greater than during the 1939 growing season: 69 mm. in 1940, compared to 15 in 1939. Elongation in 1939 had already begun by the time the first

[1] Acknowledgment is given to George S. Meagher for initiation of the study and collection of the data.

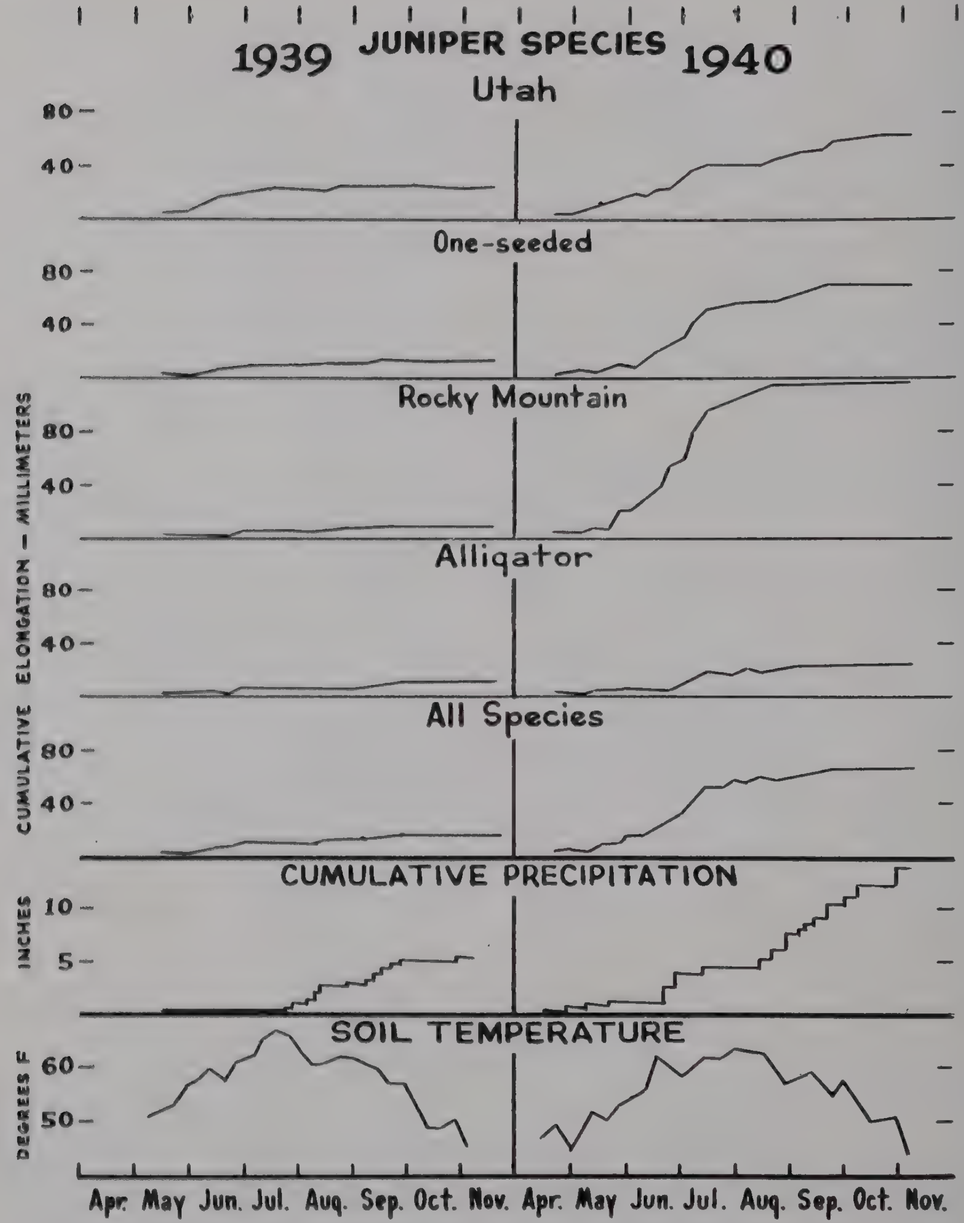

Fig. 1. Seasonal elongation of juniper leaders in relation to rainfall and soil temperature. In 1939, measurements from 3 trees, and in 1940, from 5 trees, of each species were averaged.

measurement was taken; however, it is believed that only a limited amount of growth had taken place prior to study establishment.

There is a close relationship between growth and rainfall within each season for each of the species. Evidently the reserve soil moisture from winter precipitation was sufficient to carry growth through a primary period to early summer. Each year, this primary growth period was followed by 3 to 4 weeks of negligible growth, with the exception for some unaccountable reason of 1940 growth of Rocky Mountain juniper. There was little or no rain during this time and soil moisture had presumably been depleted by active transpiration and evaporation. Growth was resumed each year following the first good rains in August but gradually slowed as the end of the growing season approached. The capacity of these native junipers to cease active growth soon after moisture conditions are unfavorable and resume growth when moisture again becomes available may account for their ability to survive on dry, exposed sites. Seasonal growth fluctuations may also account for the formation of false rings which are characteristic of the wood of the Southwestern junipers.

The beginnings and endings of leader elongation for both growing seasons were apparently determined by soil temperature. Incomplete data for the beginnings of growth indicated that elongation began when the soil temperature warmed to approximately 50° F. Rate of elongation steadily increased as soil temperature increased and then slowed as moisture became critical. During both growing seasons when the soil temperature was in excess of 60° F., increases in precipitation were reflected in increased rates of elongation. Toward the end of the growing seasons as soil temperature decreased below 60° F., elongation rates decreased and ultimately became zero when a temperature of approximately 50° F. was reached. This pattern of decreasing elongation rates occurred even though moisture was seemingly sufficient to sustain a good rate of growth.

Table I. Phenological observations for four Arizona junipers, 1940 (date of occurrence)

Phenological stage	Juniper species			
	Utah	One-seed	Rocky Mountain	Alligator
Bark begins to slip	Mar. 25	Mar. 25	Apr. 8	Apr. 1
Pollen shedding and ♀ flowers open	Mar. 25	Mar. 25	Apr. 15	Apr. 8
Approximate start of leader elongation	Apr. 20	Apr. 20	Apr. 20	Apr. 20
First conspicuous formation of ♂ flowers	Aug. 19	Aug. 19	Aug. 26	Aug. 19
Bark begins to stick	Sept. 15	Sept. 15	Sept. 15	Sept. 15
Leader elongation ceases	Oct. 19	Oct. 26	Oct. 19	Oct. 19

Some additional phenological phenomena for the four species of juniper were observed in 1940. Table I shows a number of events with their dates of occurrence.

Unfortunately dates of fruit ripening and seed dispersal were not observed. However, some information about these phenomena is available in other publications.[2]

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[2] *E.g.*, Woody-plant seed manual. U. S. Dept. Agric. Misc. Publication 654, June, 1948, p. 206.

RELATION OF SAW-PALMETTO TO LONGLEAF PINE REPRODUCTION ON A DRY SITE

In a study of longleaf pine (*Pinus palustris* Mill.) reproduction on a dry ridge in southern Mississippi, seedlings were found only near clumps of saw-palmetto (*Serenoa repens* (Bartr.) Small).

The soil on this particular ridge is Norfolk sand. The openings between the saw-palmetto clumps (Fig. 1) have a sparse vegetation dominated by slender bluestem (*Andropogon tener* (Nees) Kunth), little bluestem (*A. scoparius* Michx.), sage (*Clinopodium coccineum* (Nutt.) Kuntze), and prickly pear (*Opuntia vulgaris* Mill.). There are also some bluejack oaks (*Quercus incana* Bartr.), blackjack oaks (*Q. marilandica* Muench.), and scattered longleaf pines up to 15 inches in diameter.

The distribution of longleaf pine seedlings was studied in 10 openings ranging from 7 to 28 feet in diameter. Most of the seedlings were 5 years old and none had started height growth.

The 10 plots had a total of 165 seedlings, or the equivalent of about 4,000 per acre. Instead of being evenly distributed, however, the seedlings were concentrated in the outer portions of the plots—*i.e.*, near the palmetto. In the average opening (15.2 feet in diameter), 59 per cent of them were within one foot of the base of a palmetto plant, or in the outer 25 per cent of the open area. Eighty-eight per cent were within 2 feet of the palmetto or in the outer 46 per cent of the area; and 95 per cent were within 3 feet, or in the outer 63 per cent. This is very significantly different from a uniform distribution and is a pattern that remains about the same regardless of the size of opening. Sixty-two per cent of the seedlings were found in the southern half of the openings.

Why are most of the seedlings found near the palmetto? It does not seem probable that more seed lodged there nor that predators would have eaten only the seed in the center of the openings. More likely, the shade of the palmetto protects the seedlings from lethal temperatures and improves water relations. The survival of planted longleaf pine seedlings on this site was distinctly improved by partial shading (Allen 1954).

An additional observation was made on all of the longleaf pine saplings growing on several acres of this sandy ridge. There were only 9, but 7 of them were within 2 feet of the palmetto and only one was more than 3 feet away.

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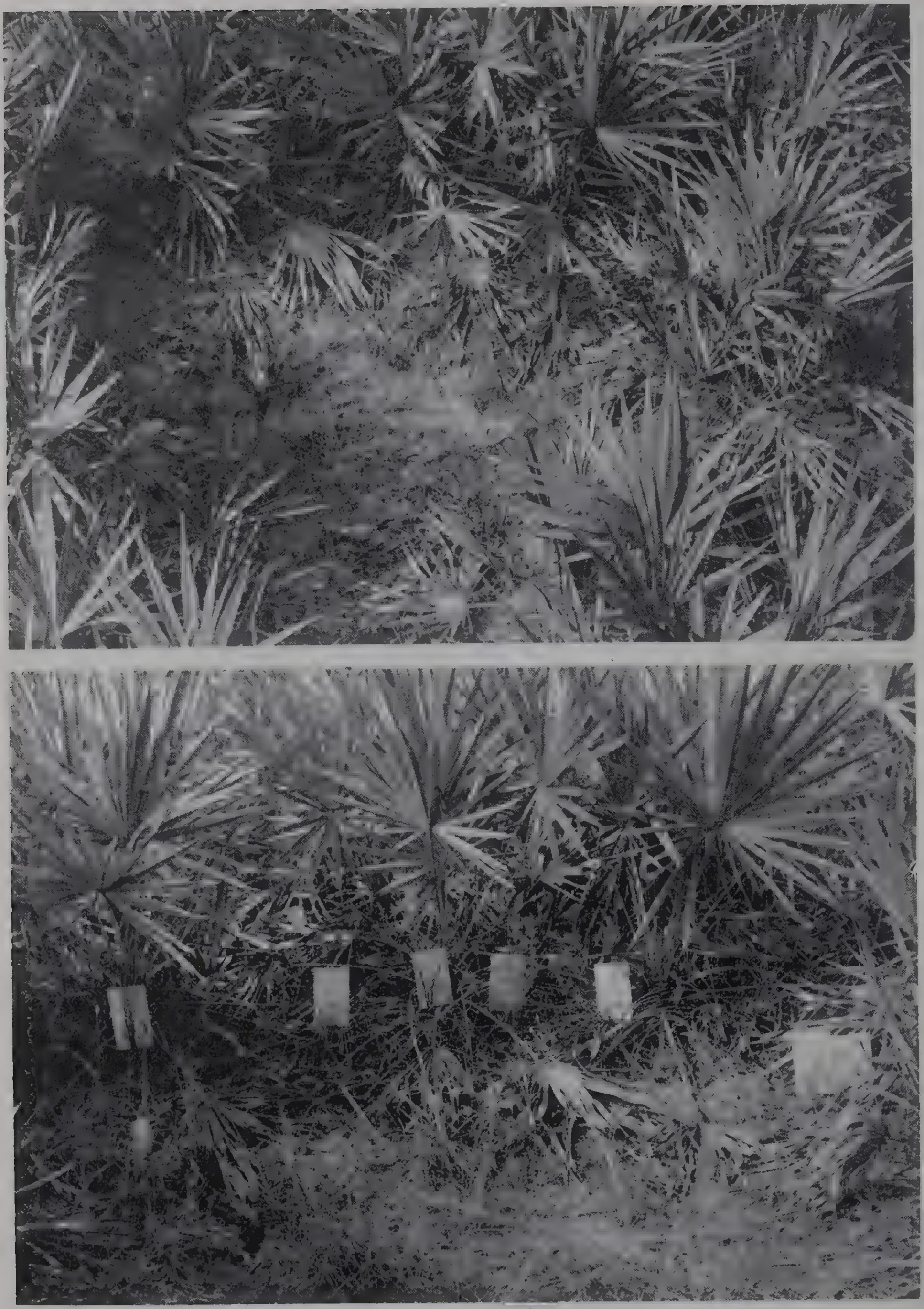

FIG. 1. *Above:* Typical small opening in the saw-palmetto. *Below:* The longleaf pine seedlings, marked by white cards, are found in the shade near the palmetto.

FUNGUS-GROWING ANTS AND THEIR FUNGI: *TRACHYMYRMEX SEPTENTRIONALIS SEMINOLE*

Trachymyrmex septentrionalis McCook is the northernmost of the tribe of fungus-growing ants, the Attini, which is exclusively American and primarily tropical. Recent studies of the species (Weber 1955, 1956) contain references to the literature. The subspecies *T.s. seminole* Wheeler is primarily an ant of the southeastern United States. The previous literature (Muesebeck *et al.* 1951) dealt with the taxonomy and summer habits.

The present studies[1] are based on material from the Archbold Biological Station in south-central Florida in August and December 1954, some of which was brought alive to Swarthmore College for further study. Attention was concentrated primarily on the habits of the ants as they affect the maintenance of the garden, on the fungus itself and on a comparison with the species as found at the northern periphery of its range. It will be seen that the Florida and New Jersey ants are indeed closely related forms when they will adopt each other's fungus-garden or pure fungus, artificially cultured. It may well be that the Florida form does not deserve subspecific rank but that is not a subject here.

HABITAT

Trachymyrmex septentrionalis seminole is distributed over the nearly two square miles comprising the Archbold Biological Station, although occupying a precise ecological habitat. The whole area is sandy and covered with pine-palmetto-scrub oak forest. Where this forest is dense the ants were not found, nor were they seen in pure stands of long-needled pine, *Pinus elliotti* Engelm, where the ground was heavily carpeted with leaves. The cultivated lawns were equally unsuitable. The ants showed a marked preference for the most open areas where the sandy surface was largely exposed. Numerous fire lines, several meters wide, kept open through the reserve were particularly favorable and showed the greatest numbers of the ant craters. From these open nesting sites they foraged into the adjacent scrub forest for substrate. The dominant plants included a short-needled pine, (*Pinus clausa* (Engelm.)), two palmettoes (*Sabal etonia* Swingle and *Serenoa repens* (Batr.)), scrub oaks (including *Quercus myrtifolia* Willd.), the turkey oak, *Quercus laevis* Walt., and the hickory, *Carya floridana* Sarg.

NEST

The external indication of the nest[2] is a bare hole, 4-5 mm in diameter, that is often concealed under fallen pine needles or other leaves, and a semicircular crater whose crest is frequently 10-12 cm distant from the hole. The intervening space is free of sand grains and renders the location of the entrance still more inconspicuous. The crater, of coarse sand grains, usually contrasted strikingly with the surrounding white sand since it was of yellow sand in nearly all cases on this reserve.

A tunnel leads at an angle from the entrance to the chamber containing the fungus garden. Only one chamber appeared to be in use in August, 1954 during the relatively dry conditions then prevailing and this was at a depth varying from 16 to 30 cm. The species may form up to seven chambers under other conditions, usually in series or with two branching off at the same level from the main descending tunnel. With one exception the chamber containing the fungus garden was excavated in yellow sand and this was, of course, moist or the ants would have gone still deeper. Indeed, in a few instances excavations to 40-50 cm beneath the crater in all directions did not reach the fungus garden. A short distance below the crater entrance may be the remains of the initial chamber excavated by the newly fecundated female and her first broods.

The fungus garden, always suspended to a large extent on rootlets, is mostly gray to grayish brown in color and is highly friable so that the generally cellular condition is destroyed upon removal. Brood is kept in these cells. The extent to which the fungus garden fills the chamber depends on the age and condition of the ant colony.

ADAPTATIONS TO THE WINTER CLIMATE

The literature on *T.s. seminole*, as with the northern form, deals only with the nesting and other habits during the summer when the ants are most active. A brief visit to the Archbold Biological Station in December, 1954 afforded an opportunity to ascertain the adaptations to the coldest weather of the year. Since this was also the dry season here, the effects may be partly due to the combination of cold and dryness. Observations were made December 20-26. The last previous rain was December 18 (about 2.5 cm). Frosts occurred early on the 21st and 22d, reaching a low of —2° C when taken under standard meteorological procedures. The temperature of the frostry grass at 7 a.m. was 0° C on the 21st, probably close to the minimum soil surface temperature, though slight differences here in exposure, nature of soil and elevation produce marked differences in temperatures during frosts, according to Mr. Archbold.

During these winter conditions many of the nests showed no above-soil surface activity, as indicated by the closure of the nest opening and the erosion of the craters by the weather. General activity of the species is usually indicated by fresh sand grains on the crater and these were absent on some, even when the entrance was open. Other nests, however, did show some activity, probably of an intermittent nature, and recently excavated sand grains were found on craters of a few.

Temperatures and fungus-chamber depths for nests are presented in Table I.

The ants of Nest No. 3411 had a garden in the form of wet, golden-brown substrate with no hyphae visible to the naked eye. The ants could crawl sluggishly when removed. They had been clustered in small knots in various places on rootlets. At a depth here of 70 cm from the surface the temperature was 15° C. At 9 a.m. the next day at this site the surface temperature had dropped to 6.2° C and the air temperature at a height of 100 cm was 8° C.

The ants were brought into the laboratory and within the next 22 hours (18.4-19.5° C) the ants built up small gardens over which were scattered loose bromatia and a few long hyphae. This suggests that the bromatia are

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[1] I am grateful to the Archbold Biological Station and Mr. Richard Archbold for making this field work possible and for the facilities so freely extended. Supplemental material was received from Mr. Leonard Brass of the same station.

[2] Photographs and descriptions of the nest of *T.s. seminole* in Mississippi appear in Cole, A. C., 1939, Lloydia, 2: 153-160. Occasionally the crater entrance may be in the form of a turret, as is not unusual in tropical *Trachymyrmex*.

TABLE I. Florida winter conditions of nests of *T. s. seminole*

Nest Number	Temperatures, °C.			Other Factors			
	Air 100 cm	Soil Surface	Fungus Cell	Depth of Cell	Day	Time	Activity**
3411......	10	12.6	13.7	20 cm	Dec. 20	10:30 a.m.	nil
3412......	13.2-.5	14.2-19.5*	13.5	22.5 cm	Dec. 20	1.25 p.m.	nil
3414......	12.7-13	14.7	14.3	24 cm	Dec. 21	4:50 p.m.	excavating
3415......	......	22.5	15.3	17.5 cm	Dec. 22	2:30 p.m.	excavating
3416......	......	24	14.5	29 cm	Dec. 22	3:15 p.m.	foraging
3417......	......	21.6-30*	14.2	25 cm	Dec. 24	3:00 p.m.	foraging
3418......	23	23.4-24.2	13.4	23 cm	Dec. 24	3:45 p.m.	foraging
3422......	......	22.8-25*	....	25 cm	Dec. 26	4:07 p.m.	foraging
3423......	......	23	18.3	19 cm	Dec. 26	4:30 p.m.	foraging

*Higher figure when sun shone here. **On the soil surface.

the form of the fungus that survives lowered temperatures and that hyphae quickly develop as it becomes warmer.

The ants of No. 3412 had a garden consisting of a few strands in the mostly empty cell. There were several clusters of ants. The fungus was in the form of long, loose hyphae and very loose bromatia, atypical of the summer condition. The substrate was dark brown in color. Twenty-two hours later, in the laboratory, the garden had become more luxuriant, with the hyphae growing markedly although the bromatia were as before.

Nests No. 3415 and 3416 were close to the site of No. 3412 and it will be noted that the sand below the surface had warmed slightly in the two-day interval. The ants had been excavating and had also developed a fungus garden on moist, brown substrate that was much more normal in appearance than before. There was no brood.

Nest No. 3417 contained ants which at 14.2° C were clustered together torpidly. They slowly uncurled and walked about when placed on a 22° surface. The ants were in an otherwise empty cell and there was no chamber to a depth of 50 cm (temperature 14.6° C). Nest No. 3418 had small fragments of a garden suspended on largely horizontal rootlets. December 26 was a warm day and the ants of No. 3422 and 3423 nests were running actively on 23° soil. There was still little foraging, and winter activity must be sporadic and not leading to the production of a garden luxuriant enough to support a generally active colony with brood.

Only single cells were found to depths of 50 cm and it is possible that there were additional and deeper cells in some cases. The ones found, however, were adequate to carry the colony over the winter and were 3.5 to 7 cm in diameter, most commonly 6 to 7 cm. If the gardens had really disappeared in those nests which contained ants only, a high mortality is indicated that is in line with data on bird, mammal and other animal populations during the winter.

The intermittent activity through the Florida winter contrasts with the complete cessation in New Jersey from October to April. The lack of full-size fungus gardens and of a brood during this period shows an adaptation similar to the northern form and is quite unlike the habits of the tropical *Trachymyrmex*. The fungus throughout this range shows an ability to cease growth and it may be the bromatial form that carries the fungus over these unfavorable periods in the north, and bromatia with some hyphae in the south.

A small test of the relations between workers of the two forms was made in the Station. Three New Jersey ants were relased on a sunny crater with a surface temperature of 26-28.5° C. One went down the nest entrance twice for a moment, only to return quickly when an ant of the nest appeared at the entrance. A second ant had the same experience and there was immediate hostility shown on both occasions. The behavior of other New Jersey and Florida ants was the same at the same temperature and they were equally sluggish below 18° C. Both forms responded quickly with warming in the laboratory.

OBSERVATION NESTS

Portions of nests were kept in containers in the laboratory for more detailed examination and experimentation.

During August the gardens contained brood that generally was covered with mycelium. Large larvae may bear numerous tufts of mycelium, and eggs may be in densely covered clusters of 10-20. The ants carefully lick the integument of the brood and go over all irregularities of the pupae, which are not enclosed in a coccoon in Attini. Callow workers are as active as mature ones and had as much integumentary bloom. Mature workers not covered with the bloom were markedly darker in color.

Sand was always removed from the vicinity of the gardens. The gardens were generally suspended from the ceiling of the container as well as from rootlets gathered with the nest. The substrate was of diverse origin, some particles being yellow to tan in color, others dark brown to black. When the ants were given a selection of partly dried to dry leaf fragments of palmetto, pine, hickory and other leaves they preferred the slightly green sections of the hickory. Semi-circular cuts were made as in Atta and *Acromyrmex*. In cutting out a section, an ant stands on one edge of the leaf, where it engages a mandible (the right one in several instances) and then uses the opposing mandible as a fulcrum, sawing back and forth (again with the right one in the above instances). By standing in one place and using the body as a radius, a semi-circular or greater section is produced whose size varies with the length and position taken by the ants. When smaller fragments are cut, the shape is highly variable and linear sections may be taken. When the piece has been cut the ant walks off, holding the narrow end forward between the mandibles and the larger part over the head and thorax. All pieces were gone over minutely, the ants licking them repeatedly.

Nests of *Cyphomyrmex rimosus minutus* Mayr in Florida commonly had mites and these were frequently watched while riding on the ants. The association between the mites and *T.s. seminole* was much less common though larger, apparently mature, ovate and brown mites were seen on several workers. One mite was attached to a leg, another to a pronotal spine. Mites were present in the gardens in nature both in August and in December. A mite that transferred from one worker ant to another and a mite that was taken from a *T.s. seminole* larva, both in August, were identified by Dr. G. W. Wharton as *Garmania* sp. (Phytoseiidae).

Fragments of nests of one colony were successfully merged with those of another on various occasions and the fungus garden of one colony would always be accepted by ants from another. The colonies used for these tests came from within the Archbold Station but were clearly independent of each other in nature.

FRAGMENTS OF NESTS ON AGAR PLATES

Experiments were conducted with fragments of colonies of *T.s. seminole* and their gardens in sterile Sabouraud's agar Petri dishes. Alien fungi and bacteria, inevitably introduced, at once started proliferating.

Usually the ants immediately took control of their fragments of fungus-gardens and successfully maintained them in the pure condition while the contaminants were growing on all sides. As in sand dishes, the ants would sometimes remove the agar on the periphery though sometimes this was left intact and an uncontaminated zone was maintained on the peripheral agar.

PURE CULTURES OF FUNGI

A pure culture was obtained on Sabouraud's agar from a fungus garden taken December 20. The garden contained long, straggly hyphae and unusually loose bromatia, By January 3 the mycelium was producing bromatia more compact than those in December and similar to those in the summer. Temperatures had been erratic, becoming 18-24° C the previous four days. During January and February samples of artificial cultures were returned to the ants and eaten by them. When the ants were immediately taken from a nest with garden there was no quick reaction to the fungus and the ants might instead lap the agar blocks that they would cut from the base of the growing fungus culture. When the ants were deprived of their fungus for several days, however, they instantly reacted by running to the culture as soon as they came within about a centimeter of it, beating the antennal tips rapidly on it, cutting, tugging, and lapping on the mycelium. The remains of the fungus would then be used as the nucleus of a garden and substrate added in the customary manner.

T.s. seminole AND OTHER FUNGI

Ants of *seminole* accepted without hesitation in December and following months artificially cultured fungi from a fungus garden of the New Jersey *Trachymyrmex septentrionalis* obtained in April, 1954. When a culture tube of the fungus on agar was introduced into their nest, the ants sometimes cut out the fungus and the agar beneath and removed the mass to a new site. They reacted favorably to artificial cultures of the Panama *Trachymyrmex cornetzi gatun* Weber, *Atta sexdens* L., *Atta cephalotes isthmicola* Weber and *Atta colombica tonsipes* Santschi fungi. These were first artificially cultured July, 1954 and given to the ants December, 1954 and later. A few ants would be introduced into agar tubes of the fungi and the ants eventually responded by cultivating the fungus, eating it and often adding blocks of agar they would cut out. No significant difference in reaction to the fungi of the three species of *Atta* was noted; all fungi were grossly similar and with well developed bromatia, larger and more compact than in *T.s. seminole.*

OTHER ANTS AND *T.s. seminole* FUNGUS

Ants of *Trachymyrmex septentrionalis* colonies accepted artificial cultures of the *T.s. seminole* fungus as did those of the Panama *Trachymyrmex urichi panamensis* Wheeler and of an *Atta sexdens* L. colony.

SUMMARY

Trachymyrmex septentrionalis seminole Wheeler is an ant of the pine-palmetto-scrub oak forest of the southeastern United States, nesting in open, sandy areas. During the Florida winter the ants maintain intermittent activity at a low ebb, generally remaining in their chambers at a depth of 17-25 cm in the sand when the temperatures here are 13-15° C. At soil surface temperatures of 22-30° C in the sun the ants may forage, though the fungus garden has a feeble hyphal development and little feeding is indicated. No brood is kept during the winter.

In the laboratory the ants quickly resumed normal activity and the fungus garden luxuriated. Brood was usually covered with mycelium in the summer. Mites (*Garmania* sp.) were sometimes present in the gardens in nature and were seen riding on the ants. Fragments of gardens with a few ants were introduced into Petri dishes containing sterile nutrient agar and the ants would maintain the garden in the pure condition despite surrounding alien fungal and bacterial colonies. The fungus was obtained in pure culture on Sabouraud's agar and produced bromatia as in the fungus garden. When returned to the ants the fungus was accepted by them as it was by other ants (*T. septentrionalis* McCook, *T. urichi panamenis* Wheeler, and *Atta sexdens* L.). The Florida *T.s. seminole* also accepted artificially cultured fungi of these species and of *Trachymyrmex cornetzi gatun* Weber, *Atta cephalotes isthmicola* Weber and *Atta colombica tonsipes* Santschi.

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EFFECT OF LIGHT INTENSITY ON THE ACTIVITY OF THE BERMUDA SPINY LOBSTER *PANULIRUS ARGUS*[1]

Fishermen have long thought that there was some relation between the size of catches of spiny lobsters and the phase of the moon. In Bermuda it is a common belief that the lobster catch (*P. argus*) is smaller on nights with bright moonlight than on dark ones. The same is claimed for *P. interruptus* in California (Allen 1916) and for *P. argus* in Florida (Crawford and DeSmidt 1922). In the latter case it was suggested that this variation was due to feeding activity correlated with the tides.

Analyses of trapping data, accumulated for an investigation of the Bermuda spiny lobster (Sutcliffe 1952, 1953), showed what seemed to be variations correlated with lunar phase. This paper presents some of the pertinent field data together with the results of laboratory experiments conducted in an attempt to explain, on the basis of light intensity, lunar variations in the trapping records.

METHODS

Field information was obtained from lobsters caught in baited traps similar to those used commercially in Bermuda (see Sutcliffe 1952). The data, which were obtained from one area of the South Shore, included records of 970 trapping over a period of 17 lunar months.

Laboratory observations were made on thirty mature lobsters of mixed sex maintained in a large indoor tank (28′ long x 3′ wide x 2′ deep) supplied with abundant running seawater. The lobsters were fed raw fish every other morning. It was found that feeding produced increased exploring or wandering activity. However, the food was usually eaten and the lobsters were relatively quiet before noon. The middle third of the tank was covered with sacking to afford a retreat or "cave" for the lobsters. The tank room, which could be completely darkened, was lighted with two fluorescent tubes providing, at water level, about 12 foot-candles measured with a standard photographic light meter. Moonlight was simulated by wrapping two spare fluorescent tubes with translucent tracing cloth until the light intensity, at water level, was somewhat less than full moonlight, as indicated by comparative measurements with a photoelectric cell and a galvanometer (uncalibrated for absolute values).

A schedule was observed with respect to lighting: The tank was brightly illuminated each day from 8-9 a.m. to about 6 p.m., and darkened completely or illuminated at the low level comparable to moonlight, from 6 p.m. until the following morning.

Counts were made at intervals of not less than a half hour between noon and midnight of the number of lobsters in the open two-thirds of the tank; a flashlight was used for counting during periods of darkness or simulated moonlight. Morning counts were not taken because of the previously mentioned feeding activity.

RESULTS

There would seem to be a correlation between the catch of lobsters and lunar phase, since the average catch was highest during new moon and lowest when the moon was full (see (Fig. 1).

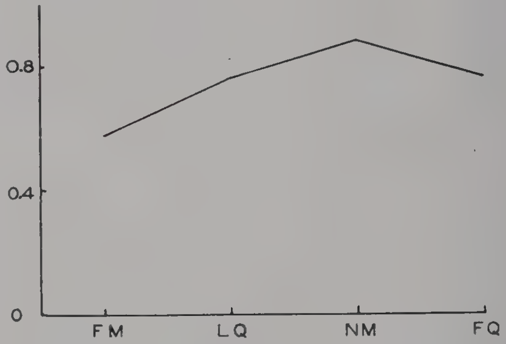

FIG. 1. Average number of lobsters per trap (ordinate) caught on the South Shore of Bermuda during various lunar phases (abscissa). Compilation of 970 trap catches (FM—233, LQ—249, NM—275, FQ—213) over a period of 17 lunar months.

The laboratory experiments were undertaken to test whether this effect was due to light. The results of the experiment indicate that there is a correlation between light intensity and activity of the captive lobsters. Table I summarizes the results, including means and standard deviations of the counts which were expressed as percentages of the number of lobsters to be expected in the open if the lobsters were totally indifferent to light. That is to say, if activity were random, one would expect to see an average of twenty lobsters in the open two thirds of the tank at all times. The counts actually observed are expressed as a percentage of the twenty lobsters in the manner used by Breder (1941) for similar experiments on fish. Statistical comparisons were made between light and moonlight groups and between the moonlight and dark groups of observations; in both cases values of t computed according to Snedecor (1946) considerably exceed theose required for significance at the 1% level.

TABLE I. Results of captive lobster counts under different conditions of illumination. Means expressed as percentages of number of lobsters expected in the open if lobsters were totally indifferent to surroundings. Tank was one-third covered and contained thirty lobsters

Condition	No. obs.	Mean %	Standard deviation
Fluorescent lights.	55	48.4	17.4
Artificial moonlight.	27	69.3	16.0
Complete darkness.	27	93.8	16.6

The activity of the captive lobsters provided several other points of interest. If no hiding place were offered, the lobsters in light tended to huddle in groups in the corners of the tank with the tails innermost to the group and the heads and antennae projecting radially. The antennae, well armed with spines, were employed quite dexterously to ward off an approaching fish or hand and, indeed, presented a rather formidable barrier when several lobsters were grouped as described. When provided with cover, most of the lobsters crowded in and might even pack quite closely together, although frequently a few lobsters (generally the larger ones) would stand at the entrance facing out with the antennae projecting into the open. This situation was also observed on several occasions in the field.

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[1] Contribution No. 223 from the Bermuda Biological of 970 trappings over a period of 17 lunar months.

When lights were turned on there was relatively little moving about; lobsters in the open would remain in one position for considerable lengths of time. At night, however, there was a great deal of activity; the lobsters constantly ranged from one end of the tank to the other and milled about with some confusion when several chanced to meet in their rounds. There was a marked diminution of such activity in simulated moonlight.

There can be little doubt that the lobsters have image or movement perception of some sort in the low light intensities of simulated moonlight, for if a hand or other object were passed over, without touching the surface of the water, they waved the antennae at the object much as in broad daylight—a characteristic and well defined response.

DISCUSSION

Panulirus argus is an animal of nocturnal habit, hiding by day in rocky holes and coming out at night to feed.[2] It is not surprising therefore, that in the clear, shallow waters around Bermuda, bright moonlight might have some inhibitory effect on noctural activity, supposing light to be the critical factor. In water of about four meters' depth or less, where most of the trapping was done for this paper, it is computed that a minimum of about 75% of the light reaches bottom for an extinction coefficient of 0.07 at Bermuda (Bumpus and Clarke 1947).

Alternative factors are direct tidal influences and internal rhythms such as found for fiddler crabs by Brown (1952). The first could hardly be the case for the water in the tank was maintained at a constant level by a stand pipe and the lobsters' behavior varied not with external tidal conditions, but with light and darkness imposed by the experiment. The same objections would seem to hold for internal rhythmicity. It should be pointed out, however, that neither of these factors can be discounted as co-operative agencies until they have been investigated fully as to their possible effects on lobsters. The agreement between field and laboratory results seems to indicate that light intensity is involved and may well underlie lunar correlations.

A consideration of interest is the possibility of the trap being used as a tool in estimates of population. It is to be noticed that the difference between the catch at full and new moon is of the same order of magnitude as that between the numbers of lobsters in the open in darkness and simulated moonlight under the experimental conditions.

SUMMARY

1. Field data from 970 trap catches of spiny lobsters (*Panulirus argus*) in Bermuda over a period of 17 lunar months and averaged according to lunar phase show that catches were highest at new moon and lowest at full moon.

2. Laboratory experiments involving similar lobsters kept in a partially covered tank agree with the field results in that more animals were counted wandering about in the open portion of the tank during periods of complete darkness than of artificial moonlight.

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[2] An exception to this is at the time of migration, when great numbers may be seen crawling over the bottom in broad daylight (Sutcliffe 1952).

MEASUREMENTS OF CONDUCTIVITY OF LAKE WATER *IN SITU*

Measurements of the total dissolved salts of lake waters are becoming increasingly useful in limnological work (Rawson 1951). The easily measured electrical conductivity of these dilute solutions is closely related to salt content (Rodhe 1949; Anderson and Pritchard 1951; Juday and Birge 1933). Moreover, changes in the carbon dioxide content made by biological activity may affect the conductivity in a way that permits useful interpretation (Ruttner 1948). The conventional measurement of conductivity involves transportation of water samples to the laboratory, and this fact puts a distinct limit on the number of measurements that can practicably be made. In connection with work on four meromictic lakes in Washington, it became necessary to determine conductivity at many depths and stations in the lakes, and an apparatus was therefore constructed for making these measurements *in situ*.

The conductivity cell, obtained from Industrial Instruments, Inc., of Cedar Grove, New Jersey, consists of two blackened platinized gold-plated nickel electrodes mounted in a hollow polystryrene cylinder 2 x 12 cm. In laboratory use the cell is dipped into the solution to be tested, the air in the cylinder being forced out through two small holes in the top as the liquid rises. Two short wires lead to connections on the bridge. In the model obtained (Cel-S2) the wires were covered by rubber tubing which fitted very tightly over the upper end of the polystyrene cylinder. The leads from the cell were lengthened by soldering the wires to a heavy rubber-covered two-conductor cable 100 feet long. The joint between the rubber tube and the rubber insulation of the cable was made watertight with several layers of electricians' rubber tape. In more than three years of frequent operation, the joint has never leaked. When the instrument is submerged, water pressure on the rubber tube puts the contained air under pressure, which then resists any tendency of water to seep in.

It was felt that there might be insufficient flushing as the cell was lowered into the lake. Therefore, the two small holes at the upper end were enlarged, and the remaining parts strengthened by plexiglass strips cemented on. In addition, a funnel was made by cutting the top off a standard 500-ml polyethylene bottle. The inside diameter of the neck is the right size to fit snugly onto the end of the conductivity cell. When the cells so modified is lowered swiftly, the water is forced through and not carried down with the cell (Fig. 1). These modifications affect the electrical properties of the cell and the cell constant must be determined by calibration with a solution of known resistance. It is necessary to calibrate the modified cell in a large vessel; a two-liter beaker is satisfactory. The constant of the cell used was changed from 2.0 to 1.4 by the modifications described.

The conductivity bridge used, a "general all-purpose instrument," obtained from the same supplier as the cell, is designated as Model RC 16. In making measurements, a knob is rotated until an electric "tuning eye" opens to a maximum extent. The resistance of the cell arm of the bridge in ohms is then read from a dial. The resistance of the sample is found by dividing by the cell constant as defined in the Operating Manual (Anonymous). In practice it is more convenient to calculate a factor which is the reciprocal of the cell constant; this factor when multiplied by the meter reading gives the specific resistance of the electrolyte. The specific conductance of the sample is then found by taking the reciprocal of the resistance. A convenient unit for limnological work is the micromho/cm, or reciprocal of megohms; a megohm is 10^6 ohms (Rosenthal 1950; Anonymous). It is understood that the resistance given is for a cube 1 cm on a side, and the unit may be given simply as micromho.

For maximum sensitivity and accuracy, the measured resistance should lie between 50 and 100,000 ohms (Rosenthal 1950). A cell of appropriate constant should be chosen on the basis of the conductivity range of the waters to be examined.

The bridge requires 110 volts A.C. current for operation. This current, not ordinarily available in rowboats, is obtained from a 6 volt automobile battery by using a vibrator-pack current converter, obtained from the same supplier.

Since resistance varies with temperature, all readings must be corrected to some standard temperature, usually taken as 18° C (Anonymous), although 25° is sometimes used. The temperature of the water must, therefore, be measured each time resistance is measured; but in any investigation to which detailed knowledge of conductivity is appropriate, equally detailed knowledge of temperature is usually needed anyway. To make the necessary measurements of temperature, a Whitney resistance thermometer was used. (Dr. L. V. Whitney, Physical Science Department, California State Polytechnic College, San Luis Obispo, California.) In earlier work, a model employing resistance wire was used, but the present model depends upon a thermistor which has a more rapid response. The Whitney instrument has an advantage over conventional resistance thermometers (Mortimer 1953) in that it reads directly in degrees. The full scale, about 8 cm, represents 5° C and the value of zero on the scale is set by a range switch. The smallest

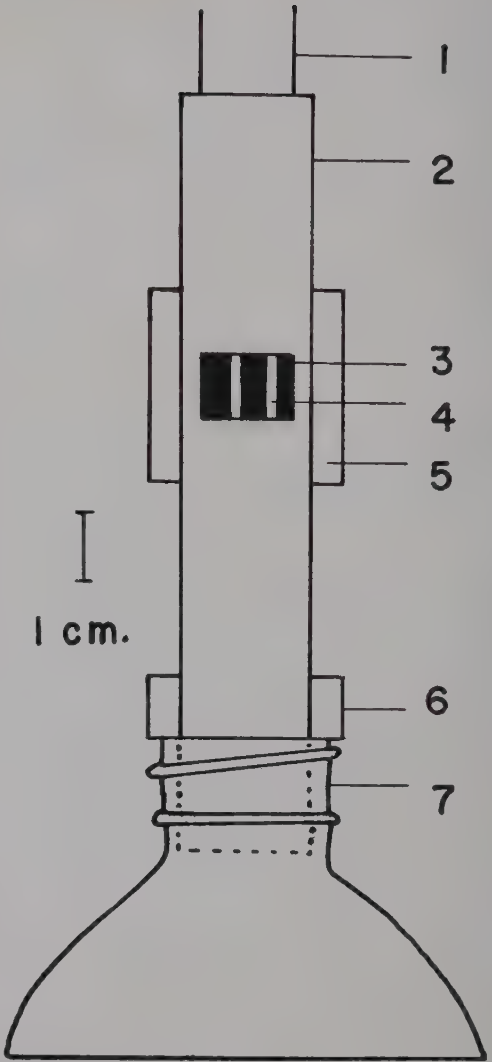

Fig. 1. Diagram of conductivity cell modified for use in lakes. 1, rubber tube covering leads from electrodes; 2, polystyrene cylinder; 3, hole cut in polystyrene cylinder; 4, electrode seen through the hole; 5, block of plexiglass cemented on for strength; 6, block of plexiglass to hold funnel in position; 7, polyethylene funnel fitted over end of cyclinder.

scale division represents 0.1° C and readings can be made securely to the nearest 0.02°C. Furthermore, controls permit the scale to be adjusted against standard thermometers, both as to the location of the zero value and the spread of the scale.

To permit convenient use of the two instruments together, the conductivity cell and thermal element are mounted close together on a bracket, and the two cables taped together and marked off at meter intervals. To make a series of readings, the boat is anchored and the underwater elements lowered successively to the depths at which measurements are to be made. At each depth the resistance is measured and recorded. Meanwhile, the thermal element has come to equilibrium. Making and recording each pair of values takes less than a minute. On a sunny day, the dark sector of the tuning eye of the conductivity bridge cannot be seen; it can be made visible by using a simple tubular shield of cardboard which fits snugly around the collar of the tuning eye and is long enough that the observer can easily apply his own eye to the upper end.

The conductivity of dilute solutions generally changes by about 2% for a change of one centigrade degree. Since it was important to know if this law was followed by the solutions being studied, the conductivity of lake water was measured at various temperatures. In one series with a temperature range from 8 to 17° C the conductivities varied from 65 to 81 micromhos, but after correction to 18° varied only from 81 to 82 which is within the error of reading.

The apparatus has been used extensively by the author and his associate, Dr. George C. Anderson, in four meromictic lakes of different kinds in Washington. Hall Lake, near Seattle, is a soft-water lake, 0.28 hectare in area and about 16 m in maximum depth. Well protected from wind by hills and trees, the lake did not mix completely during the four-year period in which it was studied and apparently had not mixed for some years previously. During most of the period, the lake had a slight inverse temperature stratification with a distinct increase in conductivity toward the bottom (Fig. 2). During windy periods, although the lake does not mix, the warmer surface water is blown downwind, and the monimolimnion (Findenegg 1935; Hutchinson 1937) becomes tilted (Figs. 3, 4). Because of the local topography, the water may be set into a rotatory motion which probably accounts for the shape of the contours in Figure 4. The data of Figure 4, based on 16 stations and comprising 227 pairs of measurements, were obtained by the author working alone in less than 5 hours. Similar observations have been made in the lake on 19 dates during a full year.

Soap Lake in arid Central Washington offers a distinct contrast to Hall Lake. It is 336 hectares in area, about 26 meters in maximum depth, and is saline. The mixolimnion has varied in salinity, particularly during the past six years. Currently it has about 23.6 gm/1 of total dissolved salts and a specific conductance of 23,980 micromhos at 18° C. The monimolimnion has a maximum of 141.2 gm/1 and 76,800 micromhos. Soap Lake too, has an inverse temperature stratification, and at one time the bottom temperature was more than 7° C warmer than the minimum temperature in the lower mixolimnion after a cold winter (Anderson 1954). The relation between conductivity and salinity is ordinarily not exactly linear, but even in Soap Lake, departure is not great within the range now existing between the two layers, and conductivity can easily be converted to salinity by means of a graph.

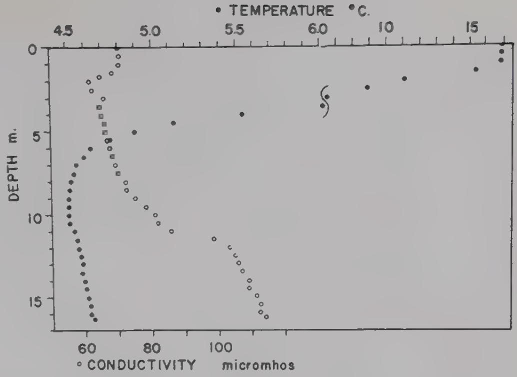

FIG. 2. Temperature and conductivity in Hall Lake on 20 May, 1952. Note the minimum conductivity at 2 m, caused by photosynthetic removal of carbon dioxide. The scale is changed above 6.0°.

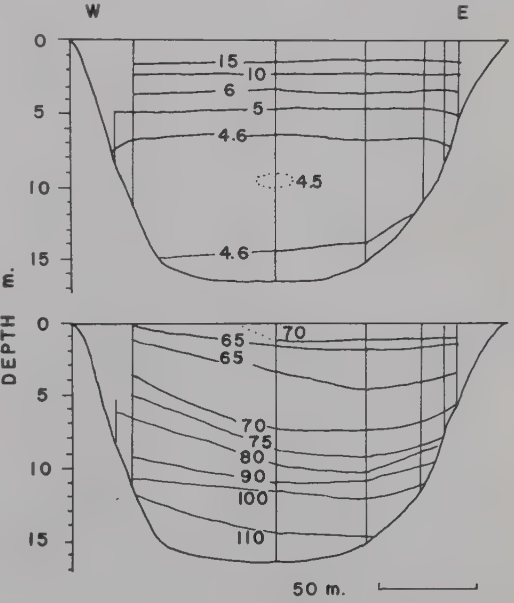

FIG. 3. Longitudinal sections of Hall Lake on 20 May, 1952, after a windy night. Above, isotherms. Note that the minimum temperature of 4.5° occurred only at the central station. Below, isopleths of conductivity. Note the two lines for 65 micromhos bounding the layer of minimum conductivity depleted by photosynthesis.

Lower Goose Lake, also in Central Washington, is remarkable for the steepness of the gradient in the chemocline. Within a quarter of a meter, the conductivity jumps from 1,600 to 8,560 micromhos at 22.5 m depth and in another quarter of a meter is 25,320. The maximum value is 40,060 at 26 m. Recently water from an irrigation canal has been turned into the lake. The extent of dilution in the upper part of the mixolimnion is plainly visible in the conductivity record.

In the fourth meromictic lake, Hot Lake in north Central Washington, currently being studied by Dr. Ander-

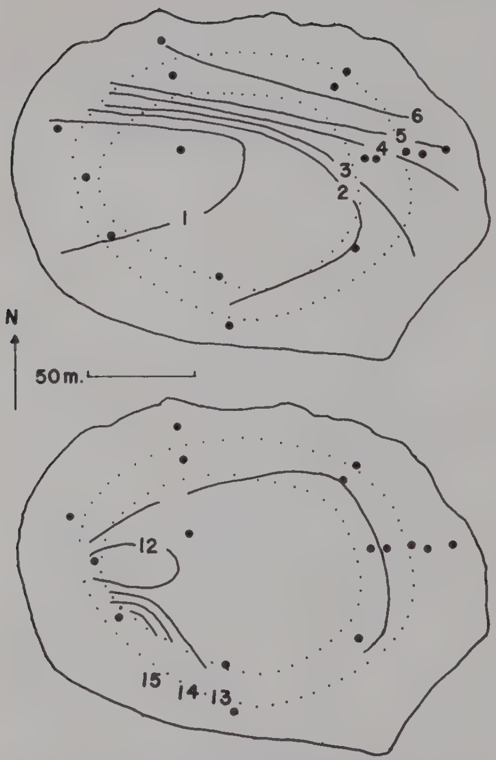

FIG. 4. Maps of Hall Lake on 29 January, 1953. The solid outline is the shore. The dotted lines are depth contours at 10 and 14 meters. Above, the solid lines are contours showing the depth at which a temperature of 5.0° C. occurred. Below, contours showing the depth at which a conductivity of 100 micromhos occurred. Contour interval in both maps is 1 meter.

son, the bottom water, at 3.2 m is nearly saturated with magnesium sulfate, and there is a fairly uniform gradient of salinity to the surface. The relations between conductivity, dilution and temperature are more complicated than in dilute solutions. The mixolimnion is thin enough that the monimolimnion is heated directly by the sun, and develops a persistent high temperature at an intermediate depth. The maximum temperature may exceed 50° C in the summer.

The author expects that further extensive use of the apparatus will be made in these lakes and believes that other limnologists would find a similar instrument useful. The cost of the conductivity section of the instrument is about $180 not including the automobile battery and the inconsequential amount of labor involved in making the connections, modifying the cell, and making a battery carrying box.

The investigations described above have been generously supported by the State of Washington Research Fund in Biology and Medicine (Initiative 171). The author wishes to acknowledge with thanks the great amount of help provided by Dr. L. V. Whitney in various ways.

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ISOPODS OF THE GENUS *LIGIA* ON THE NEW ENGLAND COAST

Shortly after daybreak on June 27, 1953, the writer observed the rocks near high tide level at Cape Neddick, Maine (approx. 43°10'N, 70°36'W) to be heavily populated with a large, fast-moving isopod. Within two hours hundreds, if not thousands, were seen. Their speed in seeking cover reminded one of the scuttling of cockroaches; and where one might see several dozen, he was fortunate to catch three or four. At about the same level on the rocks as the isopods, and sometimes intermingled with them, were numerous thysanuran insects, identified as a species of *Petrobius* by Dr. C. L. Remington of Yale University.

Subsequently, on several occasions that summer and in 1954, from early June until early October and from late May on through the summer in 1955 these animals were observed in the same place in considerable but varying numbers. On July 31, 1953, the same species was observed, secreted in crevices among the rocks at similar levels in reference to the tide on Appledore Island, Isles of Shoals, Kittery, Maine (ca. 42°60′N, 70°37′W).

Preliminary inspection of the isopods led the writer to assign them tentatively to the species *Ligia oceanica* (L.), which designation has since been confirmed by Dr. M. A. Miller of the University of California, Davis, and Dr. Fenner A. Chace of the U. S. National Museum. Through the courtesy of Torben Wolff of Universitetets Zoologiske Museum of Copenhagen the writer was able to compare some of these specimens with three different lots of *L. oceanica* from northern Europe. Although he is not an expert on isopods, he must say that he could see no obvious consistent differences between the specimens from Maine and those from Europe. Pratt's (1935) listing of this species as "very rare" in New England and Miner's (1950) complete omission of it led the writer to investigate records pertaining to its occurrence in North America. For very considerable assistance in the literature search the writer is indebted to Dr. Chace.

Gould (1841) reported a species of *Ligia* observed "about the timbers of a decaying wharf." He continues to state, "It seemed to be smaller than *L. oceanica.*" This was presumably recorded from somewhere on the coast of Massachusetts. Leidy (1855) also mentions a *Ligia* from Point Judith, R. I. Van Name (1936) suggests that these records might be of either *L. oceanica* or *L. exotica.* Richardson (1901) reports *L. oceanica* from "off Newport, R. I.;" and Blake (1931) records "a cast skin on the rocks at East Gloucester, Mass." Among the workers whom one would have expected to have collected this species had it been at all common may be mentioned Harger (1880), Kunkel (1918), and the Stephensons (1954). Harger (1880) mentions the reports of Gould and Leidy, but says he has not seen *Ligia* north of North Carolina. Kunkel does not mention the species. The Stephensons, with little doubt, know the species as it occurs in the British Isles.

A perusal of the collections at the University of New Hampshire revealed a fine, large specimen collected from Cape Neddick on June 25, 1952, by M. E. Lavoie, and two others collected "June 26, 1951, Newcastle Beach, [N.H.]" with no indication of the collector. By personal communication Dr. Lavoie assures the writer that this specimen was the only one he ever saw. Mr. James R. Miller of Pittsburgh, Pa., has informed the writer that "it occurred in large numbers throughout the summer of 1934 on the rockwork of the Duxbury (Mass.) town wharf at about high tide." His specimens were identified by Dr. Charles Blake. Miller goes on to state "They did not appear on the town wharf again, to my knowledge, although I have looked for them in other years. That same year Dr. Richard Dow of the old Boston Society of Natural History recorded it from Rockport, Mass." Dr. Chace reports (personal communication) more than 60 specimens, all collected at Newport, R. I., in 1880 by the U. S. Fish Commission, to be in the collection of the U. S. National Museum. These presumably are the basis of Richardson's report.

Thus the occurrence of this species along the New England coast appears to be a puzzle. Is it sporadic in occurrence or is its supposed rarity the result of its nocturnal habits so well understood in Europe (cf. Nicholls 1931), but perhaps not taken into account by American collectors? Although no positive answer can be given from data at hand, it would appear that the second possibility cannot possibly be the whole explanation.

In any event, it may be well to point out that *Ligia oceanica* (L.) is one of the largest isopods found in New England and that it is a species which has proven outstanding as material for experimental work. Nicholls (1931), Smith (1938), and Edney (1954) give one some idea as to the value of this species for biological study and also give one a good introduction to what has been done with it. Thus a more careful study of the rocks at high tide level with Nicholls' (1931) and Hewitt's (1907) suggestions as to methods of collection might prove rewarding. Also one cannot help but wonder whether or not the moderation of climate that appears to be in progress may not be affecting the suitability of this coast for this species. Detailed statistical comparison of relative dimensions of collections of American specimens with those from Europe might prove rewarding.

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A METHOD FOR THE SEPARATION OF SMALL BIVALVE MOLLUSCS FROM SEDIMENTS

The difficulty of separating certain bottom-dwelling aquatic organisms from the substrate sediments has long hindered progress of their study. Screening sediments fails to remove sand particles approximating the size of resident bivalve molluscs. Growth, survival, and population-density studies require that statistically significant numbers of these organisms be concentrated for counting and measurement.

A method has been developed which, after ordinary screening, permits separation of small pelecypods from the preponderately greater number of equally-sized sand particles which remain. Advantage is taken of the difference in specific gravity between the clams and sand.

The small marine clam *Gemma gemma* was used in the development of this technique. It ranges in size from 350 μ for the newly-shed fully-shelled juvenile to 5 mm in the adult organism. The reagent employed was a concentrated solution of $ZnCl_2$. The specific gravities of *Gemma* and sand collected from Raritan Bay, New Jersey, were determined and found to be 1.65 and 2.6 respectively. One hundred per cent recovery of adult *Gemma gemma* was obtained using a 75 per cent solution of $ZnCl_2$ (s.g. = 2.1).

The method essentially is as follows. After screening with water to remove as much fine particulate matter as possible, the sample is placed on a screen which holds the smallest clam present. Paper towelling is applied to the under side of the screen until water can no longer be absorbed. With a bulb pipette, the sample is flushed into a beaker with the $ZnCl_2$ solution. Enough solution is added to fill the beaker two-thirds full. The bottom material is gently stirred with a glass rod to dislodge clams held by the mass of sand particles. A few moments are allowed for settling of the sand and the raising of the clams to the surface. The clams are decanted onto the screen and the solution is saved for reuse. Water is then employed to wash the clams into a fingerbowl. The process may be repeated to remove any clams still held by the sand and adhering to the sides of the beaker, although the majority of clams are recovered in the first separation.

The concentration of the $ZnCl_2$ solution used in this separation depends on the particular species of bivalve and its size. In contrast to the results given above, 88 per cent recovery of juveniles of *Gemma g. purpurea* was achieved with an 85 per cent solution (s.g. = 2.45).

Interstitial water which is not removed by paper towelling will dilute the $ZnCl_2$ solution, but this may be corrected by adding solid $ZnCl_2$ after use.

Since the hydrolytic reaction that follows the addition of $ZnCl_2$ to water in the preparation of the solution creates a highly acid medium, shell erosion and gas evolution is to be expected. This occurs only in the umbonal region with adult *Gemma* and not at all on the external shell surface of its juveniles whose periostracum is still completely intact. Shell dimensions, however, were not perceptibly altered by leaving both adult and juvenile clams in the solution for several hours.

The solution is toxic, but this does not interfere with many aspects of the study of small infaunal bivalves.

Although further refinement and standardization of this technique are desirable, it is felt that it will be of use in its present state to workers who have sought a rapid and inexpensive method of separating small bivalves from bottom sediments.

Acknowledgment is made with thanks to Dr. M. C. Carriker, Department of Zoology, University of North Carolina, for his reading of the manuscript and many helpful suggestions and to the Rutgers University Research Council for support under Project No. 234.

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THE NATURAL HISTORY OF TSETSE FLIES[1]

"Epidemiology" could well be defined as the "ecology of disease" and there is a growing awareness among ecologists and epidemiologists of this common interest. The relationship is particularly obvious in the case of diseases caused by pathogens with an alternation of hosts—among human diseases, things like malaria, yellow fever, schistosomiasis, and trypanosomiasis. Of course all disease problems are equally ecological, in the broad sense of the word; but the purely human diseases involve the special subject of the ecology of man. When the epidemiologist starts studying insects and snails, he becomes concerned with purely biological concepts. This sort of epidemiological study has resulted in the accumulation of a very great deal of information sometimes difficult of access to biologists because of its publication in medical journals. Careful and detailed summaries of this information, like the present book by Buxton on tsetse flies, thus gain a particular importance.

Tsetse flies are of special ecological interest, quite aside from their medical importance. They must have about the lowest reproductive potential of any insect. All species are viviparous, the adult females producing single, fully grown larvae, at intervals of about 10 days. Thus, if one assumes that the average life of the female is 70 days, the average number of offspring per female will be six—a remarkable figure for any invertebrate. Considerable effort has gone into the study of tsetse populations and they were the subject of Jackson's classical work on the estimation of population size by the recapture of marked specimens. The fact that tsetse incidence is closely related to vegetation has been the direct stimulus for much investigation of the distribution of African vegetation types.

Professor Buxton starts his book with a discussion of anatomy and systematics. Twenty-one species of *Glossina* are known. One of these was not described until 1952, but Buxton considers it unlikely that further species will be discovered. The *Glossina* species should be of considerable interest to the student of the species problem because they have been rather thoroughly studied from the points of view of anatomy, variation, distribution and behavior, and because they have been the subject of numerous hybridization experiments. Their genetics, unfortunately, has not been studied. The taxonomic chapter is followed by a review of the geographical distribution of the various species. All are tropical African with the exception of *G. tachinoides,* which extends from Abyssinia and the Sudan to southern Arabia (an old, but apparently authentic record).

The succeeding chapters deal with physiological topics: "Feeding, Digestion and Excretion"; "Metabolism"; "Sense Organs: Discovery of Host"; "Sources of Food"; and "Movement and Rest." There is a great deal of material on behavior here, particularly on the finding of hosts, which seems to be primarily a visual response.

There is material of ecological interest all through the book but the chapters on "Tsetse and Climate"; "Tsetse and Vegetation"; "Reproduction"; "Larva and Puparium" "Causes of Death"; and "Populations of Tsetse" are of particular interest. Buxton has reviewed the literature on the causes of death in *Glossina* with especial care and his catalogue of tsetse hazards is probably as complete as could now be made for any insect. But the perplexing problem of getting quantitative measures of the different sorts of factors causing mortality in nature remains unsolved, even with the tsetses. These flies, however, have been the subjects of an unusual number of population studies, both under laboratory conditions and in nature, and the student of animal populations will find much of interest in Buxton's chapters on reproduction, mortality, and population dynamics.

The final chapters are on control and on the relation of the flies to disease. There are ten appendices, mostly on methods of study; a bibliography of some 600 titles; and 47 plates of photographs, mostly of tsetse habitats and of African vegetation types.

The book is perhaps primarily a basic manual for the student of tsetse flies—too detailed for the reader with only general ecological interests. But it is so well arranged and so carefully indexed that the working ecologist should have no difficulty in pulling out the information on any particular topic in which he may be interested.

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[1] Buxton, P. A. 1955. The natural history of tsetse flies; an account of the biology of the genus *Glossina*. xviii + 816 pp., 165 figs., 47 plates. London: H. K. Lewis & Company, £4-4-0.

GEOGRAPHY OF THE NORTHLANDS[1]

This reviewer (other persons perhaps have the same reaction) tends to look askance on a multiauthor book. There is the suspicion that such volumes have their origin as a gleam in an editor's eye, followed by artificial insemination of a writing herd, a suitable period of gestation, and finally by parturition with a subsidized publisher acting as midwife. Of necessity the progeny exhibits hybrid characteristics.

The book here under review rather evidently has something of this kind of background. The odium of such generation is, however, considerably relieved by the circumstance that nearly all the authors appear to have had field experience, extensive first-hand contact with the places and phenomena they write about. The over-all unfavorable impression one gets is that the pitch is promotional, Stefanssonesque, 'the northlands should and will come into their own.'

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[1] Kimble, George H. T. and Good, Dorothy, editors, and 13 other authors. 1955. Geography of the Northlands. x + 534 pp., 47 Figs. (outline maps) 75 Plates (halftone reproductions of photographs). New York: American Geographical Society and John Wiley & Sons, Inc. $10.50.

In the first line of the Preface the work is designated as a textbook. In scope it merits such classification. It is nearly equally divided into two major sections: "Systematic Studies," 13 papers, "Regional Studies," 14 papers. Under Systematic Studies" physiography, water masses, weather and climate, biogeography of the lands and inland waters, marine life, aboriginal populations, immigrant populations, transportation, wealth of the northlands (3 papers) and political aspects are discussed; under "Regional Studies" Alaska, Northwestern Canada, Eastern Canada, Canadian Arctic Archipelago, Greenland, Iceland, Svalbard and Jan Mayen, Northern Scandinavia and the U.S.S.R. (6 papers) are separately treated.

For rewarding use as a textbook the student will need first to possess a very broad background of general geography and its underlying sciences and then to make a rigorous effort in assimilating the content. In part such effort is compelled by the disjointed presentation that is a defect of a number of the pieces. What is here found fault with is exemplified in comical exaggeration in a quotation of the account given the homefolk by Haetta, a Lapp, reindeer driver, of his sojourn among the Canadian Eskimo. "The Eskimo were smart to learn but I had a free ticket so I come back. I should not come back, but I had a free ticket. They call reindeer calves 'fawns.' Not many ptarmigan, the Norwegians call them 'ryper'; too many foxes around now. Very little money from ptarmigan." He goes on further to advise "Canada is a fine place," and "The trouble with Darwin's theory is that apes have had just as long as men to learn things, but they haven't. . . ." It is not meant that the *non sequiturs* of any of the English contributors to the book are quite so hapless but they are enough so to be irritating.

Readers who turn to the book as a reference will find up-to-date data hard to come by elsewhere, but may also be frustrated by unlooked for voids in the accounts and only incidental unspecific mentions of places, phenomena, and materials that are of more than average interest. Thus there is a passing reference to the "prevailing easterlies" on page 59 in the paper on weather and climate, but no discussion and no index entry for them.

For ecologists the especially pertinent and perhaps best chapter in the book is that by Pierre Dansereau on Biogeography of the Land and Inland Waters. This heading is slightly misleading because there are only incidental general references to the fauna whereas the analysis of the environmental relationships and varying aspects of the flora are specific and complete. Of the regional studies that on Iceland by J. Brian Bird may be similarly commended.

It is regrettable that better, easily read maps were not provided, also, that Dansereau, for example, does not have one showing the circumpolar boundaries of the ice, tundra, taiga, and boreal forest belts.

To summarize: This volume, while not a source book *sensu stricto,* will serve as a well-authenticated generalized introduction to the environmental phenomena of the Northlands—one that may well be consulted when the concern is not about a particular area or species, or phenomenon since that one may not have been included in the discussions.

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Weaver's Prairie[1, 2]

Regional studies of major North American vegetation types, integrating the voluminous and scattered literature, are remarkable for their paucity. Consequently the appearence of a volume entitled NORTH AMERICAN PRAIRIE by J. E. Weaver will be greeted eagerly, and will at once find a permanent niche on library shelves.

The term "book review" covers a multitude of assumedly literary activities, creditable and discreditable. In this instance, it is my thought to pen nothing but a pointed "preface," which may allow the reader better to benefit by the book, without subjecting himself to certain lost and confused efforts that might otherwise occur.

Dr. Weaver's 38 years of activity at the University of Nebraska have almost synonymized him with prairie research. The flyleaf of the book jacket succinctly and admirably states the case, in that the book "distills the results of a lifetime's uninterrupted, laborious field research." research, unaffected and undiluted by the researches of others. When such other research is discussed, it is usu- Here is a concentrated abstracted survey of Weaverian ally segregated as carefully as are certain students in race-conscious Southern schools. Furthermore, Dr. Weaver is not a historian, and does not share the approach that James C. Malin has so excellently developed for North American grasslands. He is not a geographer, in the spirit in which Forrest Shreve served the southwestern deserts. One should also confess that Dr. Weaver is hardly a Clementsian, despite his co-siring of the Clementsian bible, for amongst many other indications, the words association, formation, sere and succession are not indexed, and the first three are not recalled from the text. The Prairie is fundamentally Dr. Weaver's prairie, and the personal knowledge he has amassed remains a most notable individualistic achievement.

The Prairie, that tall-grass eastern half of the interior North American grassland, is described in 16 chapters. By some incomprehensible slip of editorial rationality, the 3-page Table of Contents includes no page references. Since the separate text pages do not have abbreviated chapter headings, one can run down any one section only by an annoying amount of page-flipping. The segregation into chapters, in this reviewer's opinion, only veils the structure of the book, and will not be paralleled in this discussion.

The first chapter is in the nature of an Introduction (pages 3-22), and here one meets the relatively simple one-factor ecologic philosophy that the Prairie is related to limited water supply, as determined by precipitation. All other factors are directly correlated with this. The

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[1] Weaver, J. E. 1954. The North American Prairie. xi + 348 pp. 87 fig. Lincoln, Nebraska: Johnson Publishing Co. $5.00

[2] This book was reviewed by B. W. Allred in Ecology 35(4): 591, 1954. This second review is financed by funds other than those of the Ecological Society of America.

Prairie is a 25 million year old "climax," linked to this moisture situation.

The major species, their ecology, and the major "communities" are discussed in Chapters 2-5 (pages 23-85). Lowlands are handled first; then uplands. In each, grass species, grass communities, and forb species are handled separately.

A discussion of roots and rhizomes follows (Chapters 6 and 7, pages 86-117), on the floristic basis of separate discussions for each species.

Chapter 8 is a catch-all, adequately titled "Stability, Seasonal Aspects and Other Studies in Prairie."

The climatic situation is not given chapterial recognition since in a sense climate *is* prairie, and vice versa. The edaphic aspects, however, are handled in Chapter 9, "Some Plant-Soil Relationships."

Non-Weaverian contributions are congregated in Chapters 10 and 11 (pages 167-220), poorly titled "Settlement and Studies in Eastern Prairies," and "Studies in Central and Western Prairies," where they hardly even serve as do cloves on a roast ham, to season the interior. These literature abstracts are grouped by states, and neatly organized in separate paragraphs, as though copied from a card file.

What might have been entitled "The Great Drought: 1934-1940" is developed in Chapters 12-14 (pages 221-270).

The subject of Pasture Management is handled in Chapters 15 and 16 under the not-so-readily recognized captions of "Degeneration of Prairie" and "Process and Causes of Degeneration, Regeneration." Degeneration is induced by burning (the discussion is only on experimental burning) and grazing (*i.e.,* overgrazing). Regeneration involves both natural redevelopment and artificial reseeding.

The volume closes with significant words "In Retrospect," pointing out that this vast area of natural vegetation has all but disappeared, and that much can be learned from an understanding of the fragments that are left.

The 87 figures are all excellent photographs and line drawings of roots. There is a remarkable dearth of tables and graphs, charts and drawings, devices that might have portrayed pictorially much of the words of the text, and thus made for easier comprehension. There is only one map, by Transeau, of the Prairie Peninsula. Furthermore, it is quite significant that the words Indians, animals, buffalo, prairie dog, prairie chicken, and fire are not indexed, and that the relationships of these phenomena to the dynamics and equilibria of the pre-Whiteman prairie are not given distinct consideration and evaluation.

It is undoubtedly unjust to view this volume as an integration of human knowledge, botanical only, or more inclusive, of the Prairie. It is exactly what the publisher claims it to be: a distillation of the innumerable detailed researches of our tallest student of the tall grasslands of North America. In this respect, it coordinates and organizes the scientific activity of a most productive lifetime. It makes of "Weaver's Prairie" a graspable and analysable unit, previously far-flung in a hundred publications, that will be both a challenge to future researchers to emulate, and a major element for integration into some future regional study.

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UP FROM THE SEA-SQUIRTS[1]

This is a *tour de force* on the beginnings of the backboned animals. The author admits at the outset that he has "put two and two together in the hope that the total will be greater than the sum of its parts," and he ends up with a tidy sum.

In the introduction arthropod ancestors are quickly disposed of, and such queer things as the carpoid echinoderms (which the author understands to have been sessile, whereas they actually appear to have been mobile) are frowned on as possible vertebrate ancestors, and previous other speculations analyzed.

Briefly, the thesis is that the basic chordates were ascidians. The ascidian tadpole larva evolved within the group ". . . and has not been inherited from another source." Neoteny of this larva initiated a pelagic phase, some members of which entered and exploited estuaries and rivers but returned to the sea to breed. "Amphioxus is a relic of this intermediate phase and survives as a result of having become a backslider. . . ." In river systems of very early Paleozoic time the chordates developed directly to simple, unarmored forms and evolved the large freshwater vertebrate egg. *Jaymoytius* is regarded as a Silurian survivor of this stage. The ostracoderms were a side-line of the main chordate line.

The body of the work develops the paleontological, embryological, anatomical, physiological, ecological, paleoecological, hydrodynamical, and navigational aspects of the thesis. The reasoning is close, the speculation stimulating, with a wary eye for the camouflage so cleverly laid by nature over the traces of the evolutionary path. It is a pleasure to view such a tantalizing problem from so many positions.

Professor Berrill is a specialist on the ascidians, and as such might be held to incline toward his pets as vertebrate progenitors. He is well aware of this and concludes with a graceful *caveat:*

"Whether the flight of imagination outlined . . . is correctly orientated or not, it at least has the merit of continuity. It may of course merely indicate an occupational hazard involved in studying sea-squirts not wisely but too well. . . . Proof may be for ever unobtainable, and it may not matter, for here is such stuff as dreams are made on."

Here is an excellent prologue to E. H. Colbert's sequel, "Evolution of the Vertebrates," briefly reviewed here last summer.

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[1] Berrill, N. J. 1955. *The Origin of Vertebrates,* viii + 257 pp., 31 figs. Oxford: Clarendon Press. $4.00.

ELEMENTS OF CHROMATOGRAPHY[1]

The varied techniques of chromatography have now invaded most branches of science, for they are applicable to the analysis of inorganic compounds and to the separation, identification and analysis of a wide range of more complex organic molecules. This compact little book replaces an earlier, "Introduction to Chromatography" now rendered obsolete by the rapid advances in the subject. Though this book is much less detailed than others in this field, which are cited in the bibliography, it still touches upon most of the types of technique which new users will require to know and it gives the necessary introduction upon which experience, in this essentially practical and somewhat empirical subject, may be built. (A notable exception is that the increasingly useful technique of "coupled columns"—as used by Partridge and others escapes mention.)

The historical chapter is particularly noteworthy; for it traces the development of the technique, particularly as it is carried out on paper, in such a way as to give credit to works that are not widely known. Though the detailed historical references may be obtained indirectly from the bibliography these are of sufficient interest to have warranted individual citation.

The illustrations in the book are for the most part clear and instructive. However, the amino acid chromatogram reproduced in color could have been much improved by modern standards and it quite unnecessarily directs the reader to the use of ammonia and coal gas in the cabinets. It is unfortunate that color plate Fig. 28 shows columns with tapered ends in which the "funneling" of the bands toward the center of the column is conspicuous. Other figures (Fig. 8) show more desirable types of apparatus for use in column chromatography.

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[1] Williams, T. I. 1955. The Elements of Chromatography. 90 pp., 34 figs., 7 color photos. New York: Philosophical Library. $3.75.